The ammonite genera *Fagesia* and *Neoptychites* (family Vascoceratidae) in the Iberian Trough, Spain[§]

Les genres d'ammonites *Fagesia* et *Neoptychites* (famille Vascoceratidae) dans le Bassin Ibérique (Espagne)

Los géneros de ammonites *Fagesia* y *Neoptychites* (familia Vascoceratidae) en el Surco Ibérico (España)

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Abstract

The ammonites assigned to the genera *Fagesia* Pervinquière, and *Neoptychites* Kossmat, of the Wiedmann (Tübingen, Germany) and Goy, Carretero and Meléndez (Madrid, Spain) collections obtained from the Iberian Trough have been revised. New mainly lower Turonian specimens of the species *Fagesia catinus* (Mantell), *F. tevesthensis* (Peron), *F. rudra* (Stoliczka), *F. superstes* (Kossmat), *F. pachydiscoides* Spath, and *Neoptychites cephalotus* (Courtiller) have also been presented. In addition we have described one new species: *F. mortzestus*. Studies of the morphologies and the geographical and stratigraphical distributions of all these species have led to the identification of several phylogenetic relationships between them, and to distinguishing one main phase in the evolution of the family Vascoceratidae Douvillé, characterised by the dominance of *Fagesia* with *Neoptychites*.

Résumé

Ce travail présente une révision des ammonites des collections Wiedmann (Tübingen, Allemagne) et Goy, Carretero et Meléndez (Madrid, Espagne) qui proviennent du Bassin Ibérique et qui ont été assignées aux genres *Fagesia* Pervinquière et *Neoptychites* Kossmat. Sont également présentés de nouveaux exemplaires, majoritairement du Turonien inférieur, attribués aux espèces *Fagesia catinus* (Mantell), *F. tevesthensis* (Péron), *F. rudra* (Stoliczka), *F. superstes* (Kossmat), *F. pachydiscoides* Spath et *Neoptychites cephalotus* (Courtiller). Nous avons également décrit une nouvelle espèce : *F. mortzestus*. L'étude morphologique et les distributions géographiques et temporelles de ces espèces ont permis de les situer d'un point de vue phylogénétique et de distinguer une étape principale dans l'évolution de la famille Vascoceratidae Douvillé, caractérisée par la dominance de *Fagesia* avec *Neoptychites*.

Resumen

En este trabajo se ha desarrollado una revisión de los ammonites de las colecciones Wiedmann (Tübingen, Alemania) y Goy, Carretero y Meléndez (Madrid, España) procedentes del Surco Ibérico y asignados a los géneros *Fagesia* Pervinquière, y *Neoptychites* Kossmat. Se han presentado nuevos ejemplares, en su mayoría del Turoniense inferior, atribuidos a *Fagesia catinus* (Mantell), *F. tevesthensis* (Peron), *F. rudra*

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(Stoliczka), *F. superstes* (Kossmat), *F. pachydiscoides* Spath, y *Neoptychites cephalotus* (Courtiller). Igualmente, se ha descrito una nueva especie : *F. mortzestus*. El estudio de las morfologías y las distribuciones geográficas y temporales de estas especies ha permitido la identificación de varias líneas filogenéticas y de una etapa principal en la evolución de la familia Vascoceratidae Douvillé, caracterizada por el dominio de *Fagesia* con *Neoptychites*.

Keywords: Upper Cenomanian; Lower Turonian; Ammonoidea; Vascoceratidae; New species; Iberian Trough

Mots clés : Cénomanien supérieur ; Turonien inférieur ; Ammonoidea ; Vascoceratidae ; Nouvelle espèce ; Bassin Ibérique

Palabras clave : Cenomaniense superior; Turoniense inferior; Ammonoidea; Vascoceratidae; Nueva especie; Surco Ibérico

1. Introduction

This paper firstly presents a revision of the ammonites assigned to the genera *Fagesia* Pervinquière, 1907, and *Neoptychites* Kossmat, 1895, from the Iberian Trough that are held in the Universität Tübingen (UT, Germany) and the Universidad Complutense de Madrid (UCM, Spain). These centres hold the Wiedmann (JW), Goy (AG), Carretero (CM) and Meléndez (MH) palaeontological collections, which include most of the specimens of the family Vascoceratidae Douvillé, 1912, from this palaeogeographical region. Secondly, a detailed taxonomic analysis has been made of the members of these genera obtained during field works carried out for this investigation. The field works took place in the upper Cenomanian and lower Turonian outcrops situated in the localities of Puentedey (PU) and Soncillo (PS), in the north of the province of Burgos, of Fuentetoba (FT), in the centre of Soria, and of Cantalojas (CC), Galve de Sorbe (CG), Condemios (CA; CB), Somolinos (CS) and Tamajón (TA), in the north of Guadalajara, Spain (Fig. 1). Thirdly, the information obtained has made it possible to reach several conclusions concerning the taxonomy, distribution and evolution of the Vascoceratidae.

In order to establish a more precise systematic classification of the analysed taxa, we have also studied the original types attributed to this family that are held in the Museu do Instituto Geológico e Mineiro de Lisboa, Portugal, and in the MNHN Paris, France.

From a stratigraphical point of view, the ammonites presented herein have been mainly collected from the Margas de Puentedey (Floquet et al., 1982) and Margas de Picofrentes (Floquet et al., 1982) formations, deposited respectively in the inner and in the marginal environments of the platform. These formations are remarkable for containing the most complete and characteristic marls of the studied interval in the north and centre of Spain, as pointed out by Wiedmann (1960a, 1964, 1975a, 1975b, 1979), Wiedmann and Kauffman (1978), Floquet et al. (1982), Floquet (1991), Santamaría-Zabala (1991, 1992, 1995) and Segura et al. (1993), among others. The study of these formations is highly suitable, as the biostratigraphic and taxonomic information obtained from them allows inferring the evolutionary pattern followed by the Vascoceratidae during the early Turonian in the Iberian Trough.

Fig. 1. Geographic origin of the specimens presented in this paper.

2. Historical background

From the beginning of the 20th century many cephalopods have been collected from the upper Cenomanian and lower Turonian, not only in the Iberian Trough but in the whole of Spain, and assigned to the family Vascoceratidae Douvillé, 1912, by several authors. However, only a few detailed taxonomic studies of them have ever been carried out, since only a few of these specimens have been described and illustrated in an appropriate way. Among the first systematic analysis concerning the palaeontology of the upper Cenomanian and lower Turonian cephalopods in the Iberian Trough, that of Karrenberg (1935) was the most outstanding. This author described in the Outer Navarro-Cantabrian Platform and the North-Castilian Sector many new species and mentioned several taxa, some of which can be attributed to the genus *Neoptychites* Kossmat, 1895.

After collecting and studying a large number of cephalopods from the Upper Cretaceous of the Iberian Trough, Wiedmann (1960a, 1964) identified numerous ammonites. He described several new taxa in the Outer Navarro-Cantabrian Platform and the North-Castilian and Central sectors. Among the obtained specimens, many of them from Puentedey, Fuentetoba or Somolinos, this author cited a significant number of representatives of *Fagesia* Pervinquière, 1907, and *Neoptychites*. Based on the ammonite sequences obtained during his field works containing several members of the latter genus, Wiedmann (1975a) proposed some new taxa in the Upper Cretaceous of the Central Sector. In the Outer Navarro-Cantabrian Platform, the North Castilian Sector and the La Demanda Area, Wiedmann and Kauffman (1978) and Wiedmann (1979) identified a large number of ammonites attributed to *Fagesia* and *Neoptychites*.

Based on a detailed analysis of the ammonites obtained in Condemios, Somolinos and Tamajón, Meléndez-Hevia (1984) identified an important number of species, several of them belonging to the former genus. Lamolda et al. (1989) reported some members of *Fagesia* in the Turonian of the Outer Navarro-Cantabrian Platform. Floquet (1991) analysed the Upper Cretaceous geology of the northern half of the Iberian Trough and of the Basque Basin, in the north of Spain, and cited a significant number of cephalopods, including some members of these two genera, although he did not provide any figures of them.

Santamaría-Zabala (1991, 1992, 1995) studied the upper Cenomanian to Santonian ammonites from the Outer Navarro-Cantabrian Platform and the North-Castilian Sector, and identified several representatives of *Fagesia*. Taking into account the ammonites studied by this author and additional information, Martínez et al. (1996) cited the cephalopod taxa, among them several species of this genus, collected from the upper Cenomanian to Santonian of the Basque Basin, the Outer Navarro-Cantabrian Platform and the North-Castilian Sector. Lamolda et al. (1997) analysed the Cenomanian-Turonian boundary in the Outer Navarro-Cantabrian Platform, where they obtained some members of *Fagesia*. In the relatively deep-sea originating series of the Outer Navarro-Cantabrian Platform, Küchler (1998) recognised some ammonites attributed to this genus.

Recently, Barroso-Barcenilla (2004) studied the Acanthoceratidae and the cephalopod sequence from the upper Cenomanian and lower Turonian in the northern margin of the North-Castilian Sector, identifying several members of the *Fagesia* and *Neoptychites*. The palaeontological data obtained in this work were contrasted with the ones reached in the North-Castilian Sector and other regions of the Iberian Trough by Barroso-Barcenilla (2006), and the conclusions on the genera of the carried out research have been exposed in the present paper.

Other relevant contributions to the knowledge of the taxonomy and the biostratigraphy of the upper Cenomanian and lower Turonian cephalopods in the Iberian Trough were made by some authors, such as Wiedmann (1960b, 1962, 1975b), Mojica and Wiedmann (1977), Carretero-Moreno (1982), Segura and Wiedmann (1982), López and Santamaría-Zabala (1992), Gräfe and Wiedmann (1993), Segura et al. (1993), Gräfe (1994), Santamaría-Zabala and López (1996), Barroso-Barcenilla (2007) and Barroso-Barcenilla and Goy (2007).

Likewise, in the last years several biostratigraphic investigations were carried out in other palaeogeographical regions adjoining to the Iberian Trough, and closely related to it, in which Upper Cretaceous cephalopod sequences were identifi . Among these works, those by Wiese (1995, 1996, 1997), Wilmsen (1996, 1997a, 1997b, 2000), Wilmsen and Wiese (1996) and Wiese and Wilmsen (1999) in the North-Cantabrian Basin, and by Martínez (1982) in the Pyrenean Basin, both located in the north of Spain, may be cited.

3. Revision of the *Fagesia* and *Neoptychites* (Vascoceratidae) from the Iberian Trough held in the collections of the UT and the UCM

At the present time, the JW, AG, CM and MH collections of the UT and the UCM together contain the largest number of representatives of the family Vascoceratidae Douvillé, 1912, so far collected from the upper Cenomanian and lower Turonian of the Iberian Trough. However, it has not been possible to find specimens of all the members of the genera *Fagesia* Pervinquière, 1907, and *Neoptychites* Kossmat, 1895, cited in the works of Wiedmann (1960a, 1964, 1975a, 1979) and Wiedmann and Kauffman (1978) in the UT. The present investigation is based exclusively on specimens that are now hosted in the JW collection, which is why not all the representatives of these two genera mentioned in the publications of the German investigator have been revised. Likewise, it is important to indicate that the method by which the fossils of the CM collection have been numbered and identified has hindered an adequate and individualized tracking of its ammonites. Therefore, the revision of the taxa cited by Carretero-Moreno (1982) has only been partially carried out, and as a result the references to her work in the synonymy of the systematic section are imprecise.

In the present paper, the palaeogeographical division (Fig. 2) and the ammonite zonation (Fig. 3) for the upper Cenomanian and lower Turonian of the Iberian Trough proposed by Barroso-Barcenilla et al. (2008) have been followed. These authors defined several biostratigraphic units, and correlated them with ones previously recognized in the same region by other investigators, and with the standard zones.

Concerning the numeration of Wiedmann's biostratigraphic units mentioned in the present paper, a modification was made between the first and the latter works of this author. Wiedmann (1960a, 1964) considered that the Cenomanian-Turonian boundary was located between the *Metoicoceras muelleri* and the *Metoicoceras swallowi* zones. Therefore, the latter was considered as the first biostratigraphic unit of the upper stage. The location of the boundary was later modified by Wiedmann and Kauffman (1978) and Wiedmann (1979). They held the opinion that the beginning of the Turonian coincided with the appearance of the genus *Vascoceras* Choffat, 1898. On the basis of this new premise, the *Vascoceras gamai* zone was the oldest Turonian, which is why these authors began the enumeration of their biostratigraphic divisions from this unit. In order to avoid possible confusions, all references made in this paper to Wiedmann's biostratigraphic zones allude to his most recent works.

3.1. Fagesia *Pervinquière, 1907*

Wiedmann (1960a, 1964) stated that all his specimens assigned to species of the genus *Fagesia* were collected from his middle Turonian zone T VI, which he named of *Neoptychites* and *Pseudaspidoceras*. This stratigraphical distribution however seems to be too high, and Wiedmann and Kauffman (1978) and Wiedmann (1979) modified it. They

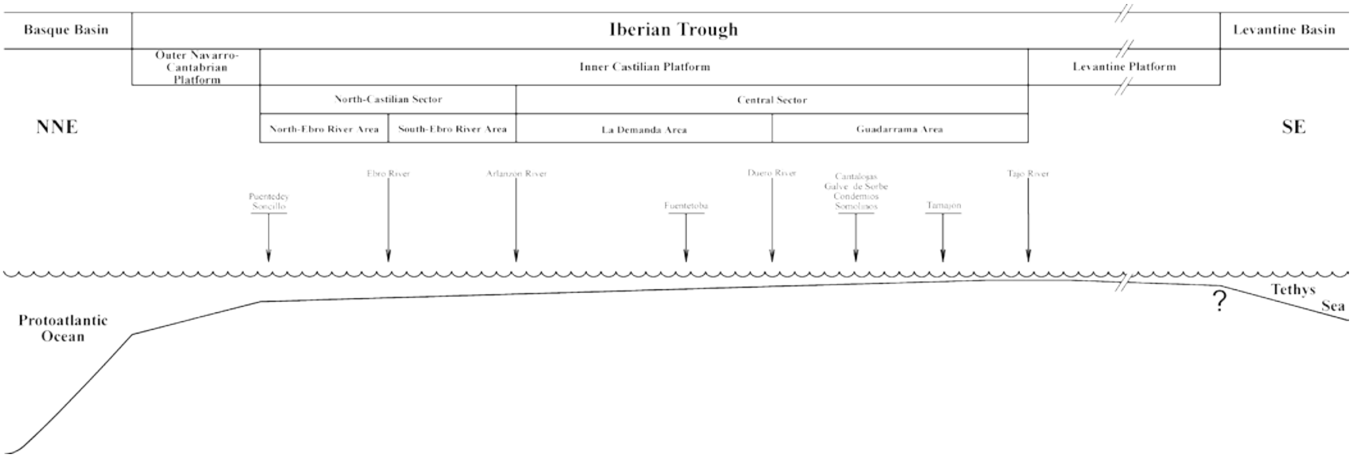

Fig. 2. Divisions followed in the Iberian Trough, with indication of the approximate location of the studied outcrops and the geographic boundaries between their different palaeogeographic areas.

established the zone T V, also named of *Fagesia* spp., within the Outer Navarro-Cantabrian Platform, on the basis of the common occurrence of the members of this genus. This new interval attributed to *Fagesia* seems more correct, and in accordance with the rest of the Spanish records of this genus obtained by other authors.

The AG and MH collections contain several ammonites, collected from the *Choffaticeras* (*Leoniceras*) *luciae* subzone and the base of the *Mammites nodosoides* zone of the Guadarrama Area, that were classified by Meléndez-Hevia (1984) as *F.* cf. *tehevensis* [sic] (Peron, 1896). Among these specimens, the ones not illustrated can easily be assigned to this

Substage	Standard ammonite zonation. Based on Kennedy (1984), Tröger & Kennedy (1996), Bengston (1996) and Gradstein et al. (2004).	North of Spain. Wiedmann & Kauffman (1978) and Wiedmann (1979).		Iberian Trough, Spain. Barroso-Barcenilla, Goy & Segura (manuscript in review). Zones	Subzones
Lower Turonian	*Mammites nodosoides*	*Wrightoceras munieri* +*Spathitoides sulcatus*	T V	*Mammites nodosoides*	*Wrightoceras munieri*
					Mammites nodosoides
	Watinoceras devonense	*Ingridella malladae* + *Schindewolfites* spp.	T IV	*Spathites* (*Ingridella*) *malladae*	*Choffaticeras* (*Leoniceras*) *luciae*
					Spathites (*Ingridella*) *malladae*
		Leoniceras discoidale + *Paramammites*? *saenzi*	T III	*Choffaticeras* (*Choffaticeras*) *quaasi*	
Upper Cenomanian	*Neocardioceras juddi*	*Fallotites subconciliatus*	T II	*Spathites* (*Jeanrogericeras*) *subconciliatus*	
	Metoicoceras geslinianum	*Vascoceras gamai*	T I	*Metoicoceras geslinianum*	*Vascoceras gamai*
		Metoicoceras geslinianum	C VII		*Metoicoceras geslinianum*
	Calycoceras (*Proeucalycoceras*) *guerangeri*	*Metoicoceras muelleri*	C VI	*Neolobites vibrayeanus*	*Metoicoceras mosbyense*
		Calycoceras (*Lotzeites*) *lotzei* + *Neolobites vibrayeanus*	C V		*Neolobites vibrayeanus*
		Eucalycoceras	C	*Eucalycoceras rowei*	*Calycoceras* (*Calycoceras*) *naviculare*
		spathi	IV		*Eucalycoceras rowei*

Fig. 3. Possible correlation of the biostratigraphic zonation followed in this work and other Spanish as well as the standard scales.

species of Peron, but the one shown in the illustration cannot be attributed to *F. tevesthensis*. This ammonite has subtriangular whorl section, narrow umbilici and marked ribs, and must therefore be remitted to *F. mortzestus* sp. nov. (see below, Section 4.4). The JW collection also includes a doubtful member of *F. tevesthensis* collected in the middle Turonian of the North-Ebro Area.

The AG collection has specimens of *F. rudra* (Stoliczka, 1865) obtained from the lower part of the *Mammites nodosoides* zone of the Guadarrama Area. In the JW, collection there is an ammonite assigned to *F. rudra* from the North-Ebro Area.

The AG and MH collections hold some specimens of *F. superstes* (Kossmat, 1897) collected from the *M. nodosoides* zone of the Guadarrama Area. The JW collection contains two ammonites located in the Outer Navarro-Cantabrian Platform and the North-Ebro Area, and classified as *F. superstes* and *F.* cf. *superstes* by Wiedmann, which were not cited by this author.

This collection also has two ammonites, attributed by Wiedmann (1960a, 1964, 1979) to *F. bomba* (Eck, 1909) and *F.* cf. *bomba*, found in the Outer Navarro-Cantabrian Platform.

3.2. Neoptychites *Kossmat, 1895*

The JW collection holds some specimens of *N. cephalotus* (Courtiller, 1860) and *N.* cf. *cephalotus*, obtained mainly from the middle Turonian zone T VI of the North-Ebro Area.

The same collection also has an ammonite from the zone T VI of the North-Ebro Area, which was classified as *N. telingaeformis* Solger, 1904, by Wiedmann, but was not previously cited.

4. New data of *Fagesia* and *Neoptychites* (Vascoceratidae) in the Iberian Trough

In this section we present a systematic description of new records of the family Vascoceratidae Douvillé, 1912, from the Iberian Trough, obtained during field works carried out by the first author. We also describe previously unpublished members of the genera *Fagesia* Pervinquière, 1907, and *Neoptychites* Kossmat, 1895, identified in the AG and MH collections.

4.1. Acronyms and abbreviations

To make clear some taxonomic comments or to indicate the location of several type specimens, the following abbreviations are used throughout the text:

- British Museum (Natural History) (BMNH), London, UK;
- Château de Saumur (CS), France;
- Universität Tübingen (UT), Germany;
- International Code of Zoological Nomenclature (ICZN);
- Musée national d'Histoire Naturelle (MNHN), Paris, France;
- Universidad Complutense de Madrid (UCM), Spain;
- Université Pierre-et-Marie-Curie (UPMC), Paris, France.

4.2. Terminology

The terminology used to describe the different specimens studied is based on the glossary of morphological terms applicable to post-Triassic nautiloids and ammonoids proposed by Barroso-Barcenilla (2008).

4.3. Dimensions and location of specimens

Measurements were made with an adjustable caliper, and are given in tenths of millimetre and as percentages of the diameter shell. The dimensions used in the analysis are defined as follows:

- diameter of the shell (D), maximum distance between two diametrically opposite ventral extremes, measured perpendicularly to the coiling axis;
- whorl height (H), maximum distance between the ventral extreme and the most distanced point of the dorsal wall, taken parallelly to the plane of bilateral symmetry;
- whorl breadth (B), maximum distance between both flanks, measured perpendicularly to the coiling axis (tubercles and ribs have not been taken into account);
- umbilical width (U), maximum distance, taken perpendicularly to the coiling axis, separating two diametrically opposite umbilical margins of the same whorl.

All the specimens presented here are held in the Departamento de Paleontología of the UCM.

4.4. Systematic palaeontology

VASCOCERATIDAE Douvillé, 1912.
[NEOPTYCHITINAE Collignon, 1965, p. 70].

Diagnosis, discussion and occurrence: a detailed analysis of the main characteristics of this family is presented by Barroso-Barcenilla and Goy (manuscript in review).

Fagesia Pervinquière, 1907

[*Plesiovascoceras* Spath, 1925, p. 198, type species by original designation *Ammonites catinus* Mantell, 1822].

Type species: *Olcostephanus superstes* Kossmat, 1897, by original designation.

Diagnosis: globose cadicones with arched ventral region, wide and deep umbilici and strong and blunt umbilical tubercles. From each of these tubercles two or three rounded ribs grow and cross the ventral region. Most of its members have a coronate section. Ornamentation usually remains unchanged until advanced ontogenetic stages. During growth some species can lose tubercles and ribs, reaching maturity with a totally smooth shell or with some occasional constrictions. The suture lines are more complex than in most vascoceratids, with many deep and narrow minor elements. Each suture line presents three or four narrow, well-developed and bifurcate lobes and marked saddles per flank, the first two of them being usually trifid and asymmetric.

Discussion: after studying some features of the suture lines of *Olcostephanus superstes* Kossmat, 1897, and comparing them with those of other members belonging to its group, Pervinquière (1907) established the genus *Fagesia* and designated this species of Kossmat as type. Eck (1909) stated that the most particular feature of *F. superstes* lies in its suture lines, more exactly in their deep incisions. Spath (1925) established the genus *Plesiovascoceras*, and included in it several evolute species with strong umbilical tubercles and ribs that disappear as they approach to the ventral region. Later on many authors, like Barber (1957), preferred to maintain the generic status of *Plesiovascoceras*, although they pointed out the important morphologic similarities with *Fagesia*. Wiedmann (1960a, 1964, 1979) attributed to *Plesiovascoceras* its own temporal distribution, slightly earlier than that which he assigned to *Fagesia*. Bengtson (1979, 1983) indicated that the type of *F. multiplex* Brito, 1971, is an Albian ammonite, probably a large member of the genus *Douvilleiceras* de Grossouvre, 1894. Wright and Kennedy (1981) remarked that *F. superstes* hardly differs from *A. catinus*, which has a slightly more involute coiling and an apparently bifid first lateral lobe. These authors stated that the characteristics indicated do not justify a generic division. After the work of Wright and Kennedy (1981) most authors, like Chancellor (1982), Kennedy et al. (1987), Chancellor et al. (1994) and Kaesler in Wright (1996), opted to include *Plesiovascoceras* within *Fagesia* as a synonym.

In recent years, several authors have studied the species that can be attributed to *Fagesia*. Kennedy and Wright (1979) assigned to this genus *F. superstes*, which shows the diagnostic features of the same group, *F. peroni* Pervinquière, 1907, *F. rudra* (Stoliczka, 1865), *F. bomba* (Eck, 1909), *F. boucheroni* (Coquand, 1859), *F. simplex* Barber, 1957, *F. catinus*, *F. involute* Barber, 1957, *F. pachydiscoides* Spath, 1925, and, as a *nomen dubium*, *F. tehevesthensis* (Peron, 1897). Chancellor (1982) stated that *F. haarmanni* Böse, 1920, should maintain its specifi status, as he considered that this species is not a synonym of *F. catinus*. He also doubted of the specifi status of *F. pachydiscoides*, and preferred to maintain *F. californica* Anderson, 1931, as a species. Kennedy et al.

(1987) regarded as conspecifi with *F. catinus* all forms of the genus identifi by Renz (1982), including *F. levis*, and modifi the number of species of the group accepted by Kennedy and Wright (1979). They considered *F. tevesthensis* and *F. pachydiscoides* as possible synonyms of *F. superstes* and *F. catinus*, respectively. The same authors accepted the specifi status of *F. lenticularis* Freund and Raab, 1969, and indicated that, as pointed out by Barber (1957), the lack of umbilical tubercles in *F. rudra*, *F. bomba* and *F. involuta*, as well as in *F. pervinquieri* Böse, 1920, could be reason enough for assigning these species to the genus *Vascoceras* Choffat, 1898. Zaborski (1987) accepted the specifi validity of *F. levis* and *F. zanelli* Etayo-Serna, 1979, and carried out an interesting analysis of the main features which differentiates the several taxa of this genus from each other. He emphasised that *F. superstes* shows ribs and strong umbilical tubercles that remain through ontogeny. *F. tevesthensis* and *F. boucheroni* lose ribs on early ontogenetic stages, as also happens with *F. peroni*, which has robust umbilical tubercles. *F. zanelli* achieves a stronger ribbing during growth. *F. bomba* and *F. involuta* develop involute coilings and *F. simplex* shows simple suture lines, but these three species soon lose their ribs. *F. lenticularis* is characterised by an eccentric and strange coiling, *F. rudra* almost lacks umbilical tubercles, and *F. pachydiscoides* has a quite compressed whorl section. Finally, the same author indicated that the umbilical tubercles of *F. catinus* become more robust during ontogeny, being maintained until adult age, and that the globose shell of *F. levis* presents slightly evolute coiling and relatively spacious ribbing. Chancellor et al. (1994) maintained the specifi status of *F. tevesthensis*, and considered *F. bomba* as a mere synonym of *F. superstes*, whose specimens are not distinguishable from the globose members of this taxon. They indicated the differing features among *F. haarmanni*, *F. californica* and *F. shastensis* Anderson, 1931, and accepted the inclusion of *F. pervinquieri* and *F. simplex* within *Vascoceras*, due to the simplicity of their suture lines. The same authors remarked that the almost unknown species *F. lenticularis* has numerous similarities with *F. rudra*. They added that the strange asymmetric coiling of *F. lenticularis* could have been caused by post mortem deformations, and suggested that *F. multiplex* seems to be an eroded puzosid. Finally, Chancellor et al. (1994) identifi the strange species *F. fleuryi* Pervinquière, 1907, although they indicated that it should be considered a *nomen dubium* and assigned to other genera of the Vascoceratidae Douvillé, 1912, due to its lack of tubercles.

Concerning the phylogeny of *Fagesia*, Wright and Kennedy (1981) stated that the sharp aspect of the ventrolateral margins of some specimens of this group could be caused by the possible proximity of the genus of Pervinquière to the subgenus *Spathites* (*Jeanrogericeras*) Wiedmann, 1960a. However, they added that the representatives of *S.* (*Jeanrogericeras*) have a double line of ventrolateral tubercles during the first ontogenetic stages, which members of *Fagesia* lack.

Occurrence: the genus *Fagesia* occurs from the upper Cenomanian to the middle Turonian of the UK, France, Spain, Portugal, North Africa, Nigeria, Cameroon, Gabon, Madagascar, the Middle East, India, the USA, Mexico, Colombia, Venezuela, Brazil and Japan. This genus is commonly considered a typical Turonian group, although Hook and Cobban (1981) and Cobban et al. (1989) seemingly collected some specimens of *Fagesia* in the upper Cenomanian *Neocardioceras juddii* zone of the USA. The palaeobiostratigraphic distribution of this genus was analysed by Matsumoto (1973) and Matsumoto and Muramoto (1978), among others. In this regard, Wright and Kennedy (1981) pointed out that *Fagesia* is one of the most widespread vascoceratids.

In the Iberian Trough, this group has been obtained in both the Outer Navarro-Cantabrian Platform and the Inner Castilian Platform. In spite of the fact that a single specimen of *Fagesia* has been found at the top of the *Spathites* (*Jeanrogericeras*) *subconciliatus* zone, a continuous record of this genus have been obtained from the upper part of the *Choffaticeras* (*Leoniceras*) *luciae* subzone to, at least, the top of the *Mammites nodosoides* zone.

Fagesia catinus (Mantell, 1822)

Fig. 4(1–3).

1822. *Ammonites catinus* – Mantell, p. 198, Pl. 22, Fig. 10 [*non* Fig. 5 (= error)].

1920. *Fagesia haarmanni* – Böse, p. 211, Pl. 14, Figs. 1, 2; Pl. 15, Fig. 2.

1923. *Vascoceras thomi* – Reeside, p. 29, Pl. 11, Figs. 1, 2; Pl. 12, Figs. 1, 2; Pl. 13, Figs. 1, 2; Pl. 14, Figs. 1, 2; Pl. 15, Figs. 1–7; Pl. 16, Figs. 1–6.

1923. *Vascoceras moultoni* – Reeside, p. 30, Pl. 17, Figs. 1, 2; Pl. 18, Figs. 1, 2.

1923. *Vascoceras stantoni* – Reeside, p. 30, Pl. 19, Figs. 1, 2; Pl. 20, Figs. 1–3; Pl. 21, Figs. 1–3.

1925. *Plesiovascoceras catinum* (Mantell) – Spath, p. 198.

1925. *Fagesia* nov. sp. – Spath, p. 198.

? 1931. *Fagesia californica* – Anderson, p. 123, Pl. 15, Fig. 1; Pl. 16, Figs. 1, 2; Pl. 17, Fig. 1, Text-Fig. 1a.

? 1931. *Fagesia shastensis* – Anderson, p. 124, Pl. 16, Fig. 3, Text-Fig. 1b.

1940. *Vascoceras* (*Pachyvascoceras*) *bernonense* – Faraud, p. 15, Pl. 7, Fig. 1; Pl. 9, Fig. 3; Pl. 10.

1954. *Fagesia haarmanni* Böse – Kummel and Decker, p. 313, Text-Fig. 3.

? 1958. *Fagesia californica* Anderson – Anderson, p. 248, Pl. 39, Figs. 1, 2.

? 1958. *Vascoceras shastense* (Anderson) – Anderson, p. 248.

? 1959. *Plesiovascoceras californicum* (Anderson) – Matsumoto, p. 102, Pl. 36, Figs. 1a–c, Text-Fig. 54a, b.

1963a. *Fagesia haarmanni* Böse – Powell, p. 320, Pl. 33, Fig. 2; Pl. 34, Figs. 1–5, Text-Fig. 2h–k.

1969. *Fagesia superstes* (Kossmat) var. *tunisiensis* Pervinquière – Thomel, p. 116, Pl. d, Figs. 1, 2; Pl. e, Figs. 1, 2.

? 1972. *Fagesia* sp. – Cobban and Scott, p. 88, Pl. 34, Figs. 1, 2; Pl. 38, Fig. 4.

1978. *Plesiovascoceras catinum* (Mantell) – Kennedy and Hancock, p. V19.

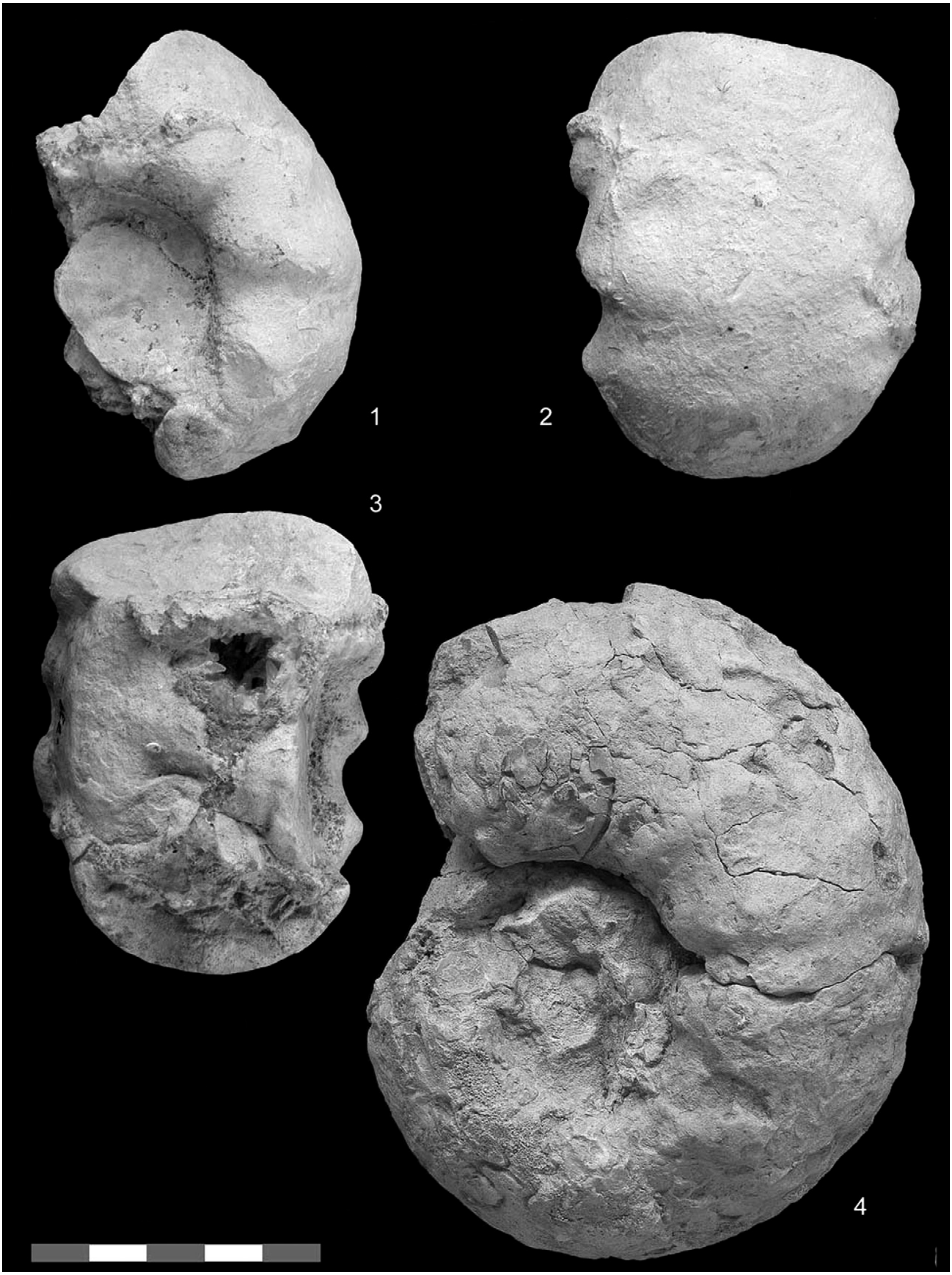

Fig. 4. 1, 2, 3. *Fagesia catinus* (Mantell, 1822), specimen FT-R-739, from an unknown lower Turonian level of Fuentetoba. 1. Lateral view. 2. Ventral view. 3. Apertural view. 4. *Fagesia tevesthensis* (Peron, 1896), specimen TA-S-585, from the *Choffaticeras* (*Leoniceras*) *luciae* subzone of Tamajón, lateral view. Bar scale = 5 cm.

1981. *Fagesia catinus* (Mantell) – Wright and Kennedy, p. 88, Pl. 26, Fig. 2, Text-Figs. 31–36.

1981. *Fagesia* or *Vascoceras* sp. – Hook and Cobban, Pl. 2, Figs. 1, 2, 5.

1986. *Fagesia catinus* (Mantell) – Kennedy, Pl. 12, Figs. 1, 2, 8, 9.

1987. *Fagesia catinus* (Mantell) – Kennedy et al., p. 51, Pl. 7, Figs. 1–11, ?12, 13; Pl. 8, Figs. 1–4, 6–9; Text-Figs. 2j, k, m, n, 10.

1989. *Fagesia catinus* (Mantell) – Cobban et al., p. 50, Figs. 50, 92l–k, 96 s, t.

1989. *Fagesia catinus* (Mantell) – Kennedy et al., p. 84.

1991. *Fagesia catinus* (Mantell) – Kennedy and Simmons, p. 141, Pl. 4c–e.

1992. *Fagesia catinus catinus* (Mantell) – Thomel, p. 229, Pl. 84, Fig. 1; Pl. 85; Pl. 86, Fig. 1; Pl. 89, Fig. 3; Pl. 90, Figs. 1, 2; Pl. ?93; Pl. ?94, Figs. 1, 2.

1994. *Fagesia catinus* (Mantell) – Kennedy, p. 260, Pl. 7, Figs. 6–8.

1994. *Fagesia catinus* (Mantell) – Kassab, p. 121, Fig. 5(8).

1996. *Fagesia catinus* (Mantell) – Kaesler in Wright, p. 176, Text-Fig. 136/1d, e.

2001. *Fagesia catinus* (Mantell) – Callapez and Ferreira, p. 86, Pl. 13, Figs. 5, 6, Text-Figs. 23.5-6.

2006. *Fagesia catinus* (Mantell) – Barroso-Barcenilla, p. 255, Pl. 35, Figs. g, h; Pl. 36, Fig. a.

Type: the holotype by monotypy is specimen C3379 of the BMNH, original of Mantell (1822: Pl. 22, Fig. 10) and collected from the lower Turonian of Lewes, UK.

Material and dimensions:

	D	H (%)	B (%)	U (%)
FT-R-739	800	246 (31)	565 (71)	322 (40)
PU-R-247	498	rv 172 (35)	rv 480 (96)	rv 150 (30)

Description: moderately involute or evolute ammonites with depressed half moon-shaped or reniform whorl section, broad venter and deep crateriform umbilici with flat and sloping walls. The smallest specimen bears 8–12 umbilical tubercles per whorl, with one or two prorsiradiate ribs arising from each of them. Likewise, some intercalated ribs can be observed in it. During ontogeny, the whorls become more evolute, umbilical width increases and ornamentation disappears, although the umbilical tubercles persist. Likewise, the ribs, which range 20–30 per spire, decline until they almost disappear.

Discussion: Wright and Kennedy (1981) carried out an interesting and detailed revision of *F. catinus* (Mantell, 1822). They refigured its holotype and some specimens of Reeside (1923) and Spath (1925), and included *F. haarmanni* Böse, 1920, *Vascoceras mohovanense* Böse, 1920, *V. thomi* Reeside, 1923, *V. moultoni* Reeside, 1923, *V. stantoni* Reeside, 1923, *F. californica* Anderson, 1931, *F. shastensis* Anderson, 1931, and *V.* (*Pachyvascoceras*) *bernonense* Faraud, 1940, within the synonymy of *F. catinus*. The same authors maintained *F. pachydiscoide*s Spath, 1925, as a separate species, on the basis of its narrower, higher and more rounded whorl section. Finally, Wright and Kennedy (1981) suggested the possible existence of sexual dimorphism in *F. catinus*. On the contrary, Chancellor (1982) considered that *F. haarmanni* presents a more involute and depressed shell with a flatter and broader venter than *F. catinus*, and observed a morphological convergence between the latter species and *F. pachydiscoides*. Kennedy et al. (1987), as well as Kennedy et al. (1989), Kennedy and Simmons (1991) and Kennedy (1994), considered *F. haarmanni*, *F. pachydiscoides* and the different taxa attributed to this genus by Renz (1982), among them *F. levis*, *F.* aff. *superstes*, *F.* cf. *tevesthensis*, *F.* aff. *F. haarmanni* and? *F.* sp., as synonyms of *F. catinus*. Zaborski (1987), on the other hand, preferred to accept the specific status of *F. levis*. Kennedy (1994) agreed with the remarks made by Kennedy et al. (1987) and added that the original description of *V.* (*P.*) *bernonense* is based on a specimen of *F. catinus* in an intermediate ontogenetic stage. Thomel (1992) found transitional specimens between *F. catinus* and *F. pachydiscoides*, and relegated the second taxa to the subspecific status, proposing his new taxon *F. catinus niciensis*. Santamaría-Zabala (1991, 1995) found that *F. catinus* has a slightly more involute coiling and a wider and less rounded whorl section than *F. pachydiscoides*, maintaining them as different species.

In fact, the types of *F. haarmanni*, *V. thomi*, *V. moultoni*, *V. stantoni*, *F.* nov. sp. of Spath (1925) and *V.* (*P.*) *bernonense* are morphologically very close to the holotype of *F. catinus*, and, therefore, these taxa seem to be mere synonyms of this species of Mantell. *F. californica* and *F. shastensis* could represent the more compressed and closer to *F. pachydiscoides* morphological extreme of *F. catinus*. Consequently, *F. californica* and *F. shastensis*, as well as the specimen of Thomel (1992: Pl. 93; Pl. 94, Figs. 1, 2), might be transitional forms between the species *F. pachydiscoides* and *F. catinus*. *V. mohovanense* exhibits coarse ornamentation, with marked ribs, and relatively depressed whorl section, and *F. levis* has spires, whose width is more than three times its height. These features differentiate *V. mohovanense* and *F. levis* from *F. catinus*, and thus we consider it reasonable to keep their specific separation. On the other hand, the features of the specimens of *F. superstes* var. *tunisiensis* Pervinquière, 1907, of Thomel (1969), with great umbilical width and virtual lack of ribs, seem to coincide with those of the members of *F. catinus*, as observed by Wright and Kennedy (1981), among other authors. Finally, immature specimens of *F.* sp. of Cobban and Scott (1972) may also possibly be assigned to *F. catinus*, but their precise taxonomic classification cannot be established since they are in early ontogenetic stages.

F. catinus, considered the type species of *Plesiovascoceras* Spath, 1925, possesses a depressed whorl section, making it difficult to distinguish from *F. superstes*. Nevertheless, the former species reaches a more evolute coiling than the latter one and loses ribbing in the early growth stages. As already emphasised by Wright and Kennedy (1981), *F. catinus* and other species of the genus differ from the most globose members of *Vascoceras* Choffat, 1898, such as *V. harttiforme* Choffat, 1898, and *V. douvillei* Choffat, 1898, in the simpler and shorter sutural elements, more involute coilings and less persistent or absent umbilical tubercles of the latters.

Occurrence: previously identified from the upper Cenomanian to the lower Turonian of the UK, Mexico, USA, Oman, France, Egypt and Portugal. *F. catinus* is the stratigraphically lowest species of the genus. Despite being characteristic of the lower Turonian, it was apparently identified by Cobban et al. (1989) in the upper Cenomanian *Neocardioceras juddii* zone of New Mexico, USA. According to Kennedy (1994), *F. catinus* is a typical boreal species. The two Spanish specimens presented herein have been collected in the Iberian Trough, specifically in levels of the upper Cenomanian *Spathites* (*Jeanrogericeras*) *subconciliatus* zone of the North-Ebro Area that were deposited during the Cenomanian-Turonian transition, and of the lower Turonian of the La Demanda Area.

Fagesia tevesthensis (Peron, 1896)

Figs. 4(4) and Fig. 5(1).

? 1860. *Ammonites alphonsi* – Coquand, p. 966.

1896. *Mammites*? *tevesthensis* – Peron, p. 23, Pl. 7, Figs. 2, 3.

cf. 1898. *Ammonites* cf. *tevesthensis* (Peron) – Choffat, p. 70, Pl. 10, Fig. 5.

? 1904. *Ammonites kotoi* – Yabe, p. 26, Pl. 6, Figs. 3, 4.

1907. *Fagesia thevestensis* (Peron) – Pervinquière, p. 325, Pl. 20, Figs. 5, 6, Text-Figs. 123, 124.

cf. 1914. *Fagesia* sp. ind. cf. *F. thevesthensis* (Peron) – Eck, p. 199.

1939. *Fagesia thevesthensis* (Peron) – Basse, p. 49.

? 1960a. *Fagesia*? *thevestensis* (Peron) – Wiedmann, p. 719.

? 1964. *Fagesia*? *thevestensis* (Peron) – Wiedmann, p. 114.

1969. *Fagesia thevesthensis* (Peron) – Freund and Raab, p. 35, Text-Fig. 7 g.

? 1969. *Fagesia* sp. – Freund and Raab, p. 42, Pl. 7, Fig. 4, Text-Fig. 9d, e.

1973. *Fagesia thevesthensis* (Peron) – Matsumoto, p. 32, Pl. 8, Fig. 2a–c, Text-Fig.? 2.

? 1979. *Fagesia*? *thevestensis* (Peron) – Wiedmann, p. 189.

non 1982. *Fagesia* cf. *thevestensis* (Peron) – Renz, p. 79, Pl. 22, Fig. 15a, b.

1984. *Fagesia* cf. *thevestensis* (Peron) – Meléndez-Hevia, p. 92 [only].

1994. *Fagesia tevesthensis* (Peron) – Kennedy, p. 261, Pl. 7, Figs. 1–4; Pl. 9, Figs. 6, 7.

1994. *Fagesia tevesthensis* (Peron) – Chancellor et al., p. 62, Pl. 15, Figs. 1–3, 10, 11.

2001. *Fagesia tevesthensis* (Peron) – Callapez and Ferreira, p. 85, Pl. 13, Figs. 1, 4, 9, 10, Text-Figs. 23.7, 23.9-10.

2006. *Fagesia tevesthensis* (Peron) – Barroso-Barcenilla, p. 258, Pl. 36, Figs. b, c.

Type: the holotype by monotypy is the specimen of Peron (1896: p. 23, Pl. 7, Figs. 2, 3), from Tebessa, Algeria, and currently held with the number J043202 in the MNHN, after being kept in the UPMC.

Material and dimensions:

	D	H (%)	B (%)	U (%)
TA-S-577	1150	398 (35)	533 (46)	475 (41)
	696	215 (31)	378 (54)	259 (37)
TA-S-585	1213	524 (43)	567 (47)	414 (34)

Description: medium-sized and slightly evolute ammonites, with depressed subreniform whorl section, rounded venter and flanks and relatively broad umbilici. Each whorl bears about 15 umbilical tubercles per flank that give rise to groups of three coarse and slightly prorsiradiate main ribs. Intercalated ribs arise among them. During ontogeny, the ribbing and the umbilical tubercles weaken.

Discussion: Peron (1897) already pointed out the difficulty of differentiating between his new species *Ammonites tevesthensis* and *Olcostephanus superstes* Kossmat, 1897, since their respective appearances are relatively close. Pervinquière (1907: Pl. 20, Fig. 5) noticed the existence of specimens with intermediate features between these two species. He also indicated that *Ammonites alphonsii* Coquand, 1860, represents an intermediate form between *F. tevesthensis* and *F. superstes*. For this reason the same author included the latter taxon in the synonymy of the former one, as did other subsequent authors such as Basse (1939). Likewise, Pervinquière (1907) and other authors, like Basse (1939), Matsumoto (1973), Kennedy (1994) and Chancellor et al. (1994), maintained that *Ammonites kotoi* Yabe, 1904, might be a conspecific form of *F. tevesthensis*. Kennedy et al. (1987) suggested that *F. tevesthensis* could be a synonym of *F. superstes*, and attributed to *F. catinus* the specimen classified by Renz (1982) as *F.* cf. *thevestensis*. Chancellor et al. (1994) indicated that the location of the original specimen of Coquand, that was never illustrated, is unknown, and therefore regarded *A. alphonsii* as a *nomen dubium*.

Regarding the separation of *F. tevesthensis* and *F. superstes*, it should be observed that the first species shows a more compressed whorl section and a more dense ribbing than the second one. Likewise, *F. superstes* has globose morphology and proportionately more reduced and deeper umbilici. Both features make it easy to distinguish between these two taxa. In the same way it can be added that, although the stratigraphical distributions of both species are relatively close and the reduced number of specimens obtained is not high enough to reach definitive conclusions, the records of *F. tevesthensis* in the Iberian Trough are lower than those of *F. superstes*. Taking into account the observations on morphology and distribution indicated above, we recommend maintaining the specific division of these two taxa. On the other hand, although the type of *A. kotoi* is an incomplete specimen in poor state of preservation, the appearance and dimensions of it seem to coincide with those of the members of *F. tevesthensis*.

The small specimen classified as *Fagesia* sp. by Freund and Raab (1969) also has the typical appearance of the representatives of *F. tevesthensis*, which is why it should probably be assigned to this species. On the contrary, the ammonite classified as *F.* cf. *thevestensis* by Renz (1982) presents a whorl section that is too depressed to be a member of the species of Peron.

Occurrence: *F. tevesthensis* occurs in the lower Turonian of Algeria, Portugal, Tunisia, Egypt, France, Israel, Japan and Spain. This species was assigned by Chancellor et al. (1994) to the *Thomasites rollandi* zone of Tunisia, which is equivalent to the upper part of the *Watinoceras devonense* standard zone. In

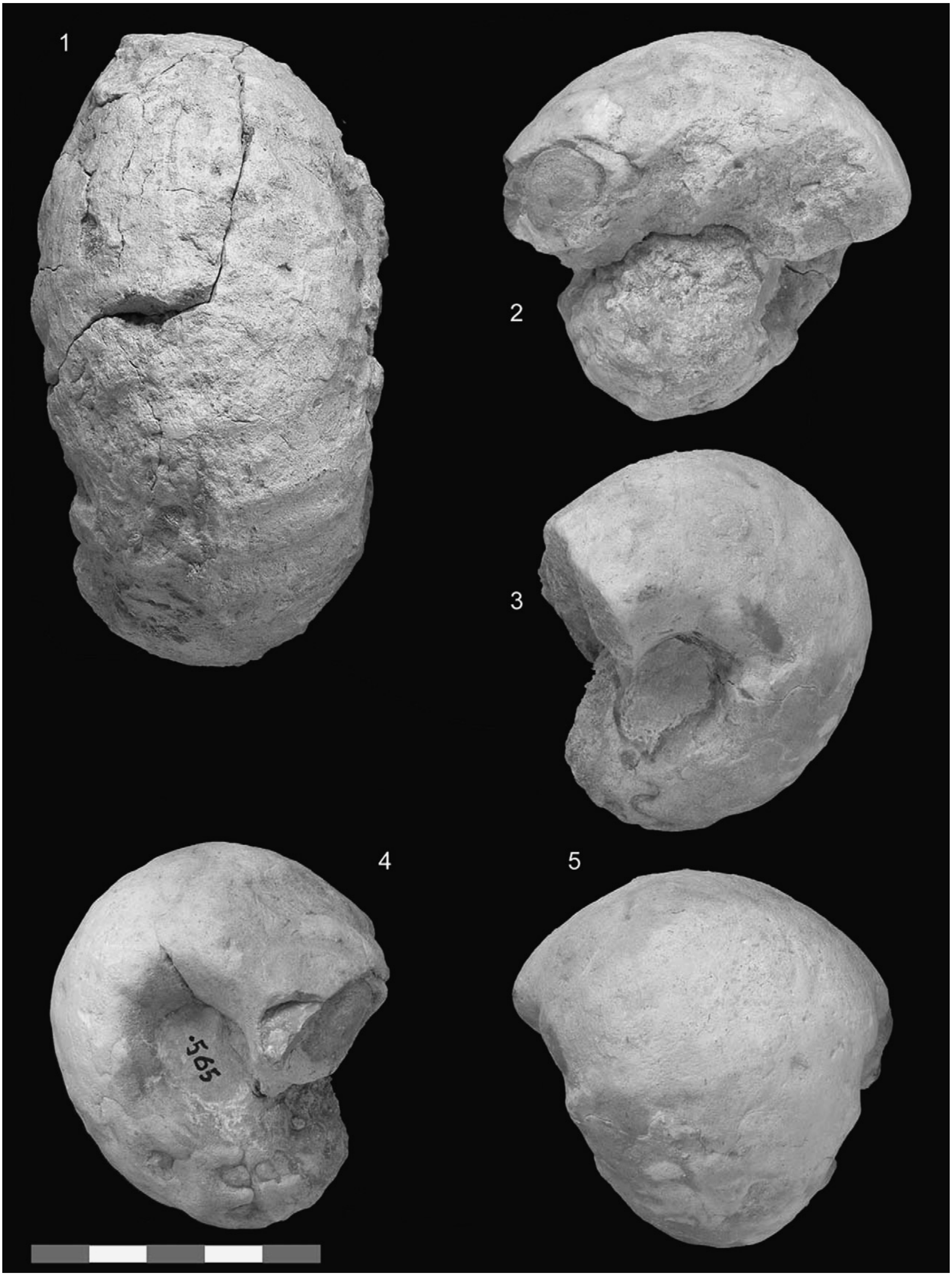

Fig. 5. 1. *Fagesia tevesthensis* (Peron, 1896), specimen TA-S-585, from the *Choffaticeras* (*Leoniceras*) *luciae* subzone of Tamajón, ventral view. 2, 3, 4, 5. *Fagesia rudra* (Stoliczka, 1865), specimen TA-S-565, from the *Mammites nodosoides* subzone of Tamajón. 2. Apertural view. 3 and 4. Lateral views. 5. Ventral view. Bar scale = 5 cm.

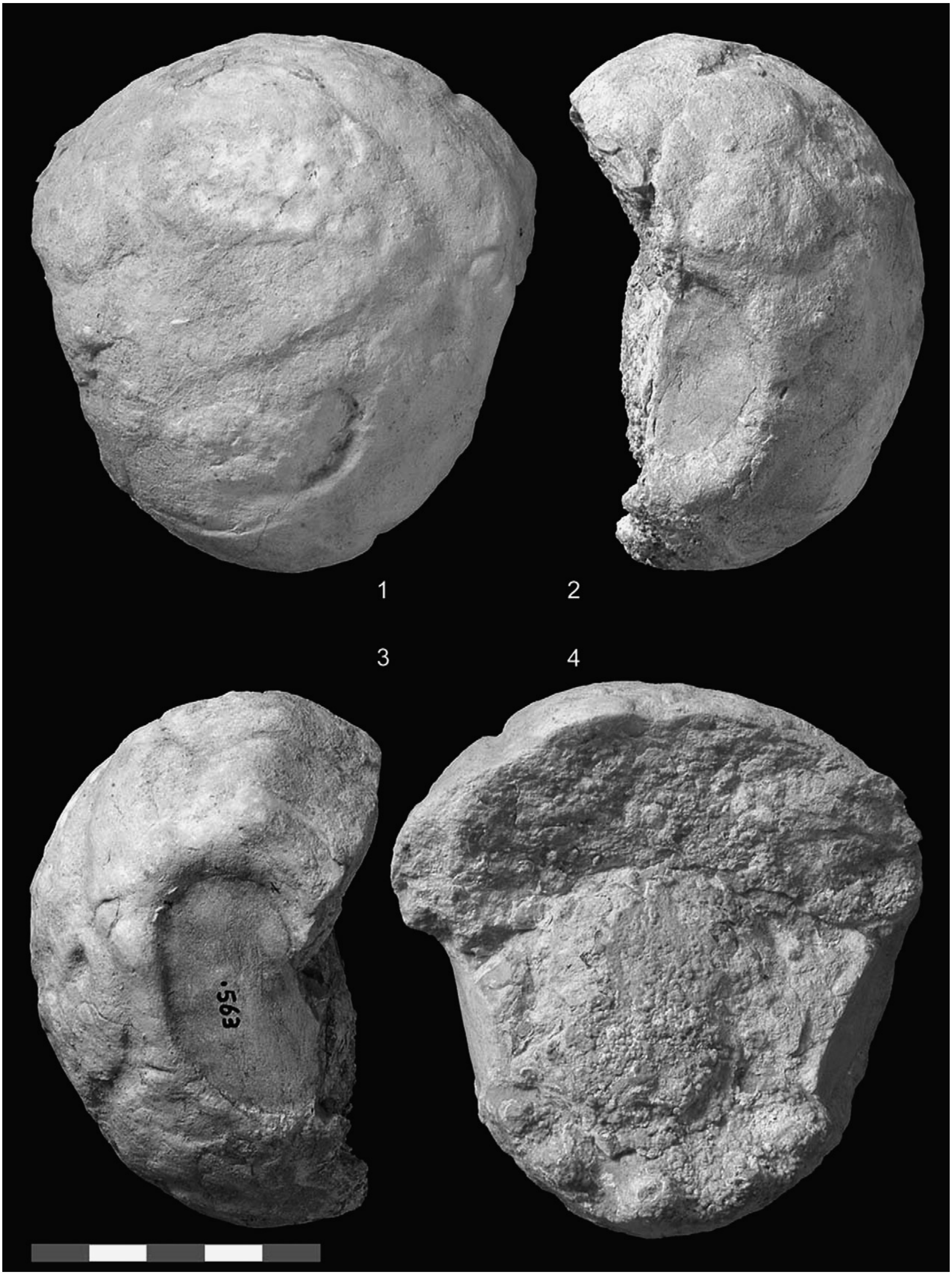

Fig. 6. *Fagesia rudra* (Stoliczka, 1865), specimen TA-S-563, from the *Mammites nodosoides* subzone of Tamajón. 1. Ventral view. 2 and 3. Lateral views. 4. Apertural view. Bar scale = 5 cm.

the Iberian Trough, it was obtained from the upper part of the *Choffaticeras* (*Leoniceras*) *luciae* subzone and the lower part of the *M. nodosoides* subzone of the North-Ebro and Guadarrama areas. Likewise, Wiedmann (1960a, 1964, 1979) cited a very doubtful specimen of *F. tevesthensis* in the middle Turonian of the North-Ebro Area.

Fagesia rudra (Stoliczka, 1865)

Fig. 5(2–5) and Fig. 6(1–4).

1865. *Ammonites rudra* – Stoliczka, p. 122, Pl. 60, Fig. 1, 1b.

1897. *Olcostephanus rudra* (Stoliczka) – Kossmat, p. 29 (136).

1960a. *Fagesia rudra* (Stoliczka) – Wiedmann, pp. 720–721.

1964. *Fagesia rudra* (Stoliczka) – Wiedmann, pp. 114–115.

1965. *Fagesia rudra* (Stoliczka) – Collignon, p. 48, Pl. 369, Fig. 1678a; Pl. 397, Fig. 1678b.

cf. 1973. *Fagesia* sp. cf. *rudra* (Stoliczka) – Matsumoto, p. 34.

1979. *Fagesia rudra* (Stoliczka) – Kennedy and Wright, p. 666, Pl. 82, Figs. 1, 2.

1984. *Fagesia rudra* (Stoliczka) – Meléndez-Hevia, p. 94, Pl. 10, Fig. 2a–c; Pl. 12, Fig. 1.

aff. 1989. *Fagesia* aff. *F. tevesthensis* (Peron) – Lamolda et al., Text-Fig. 3, Fig. 1a, b.

aff. 1991. *Fagesia* aff. *rudra* (Stoliczka) – Santamaría-Zabala, p. 153, Pl. 9, Fig. 1a, b.

aff. 1995. *Fagesia* aff. *rudra* (Stoliczka) – Santamaría-Zabala, p. 50, Pl. 2, Fig. 6.

2006. *Fagesia rudra* (Stoliczka) – Barroso-Barcenilla, p. 261, Pl. 36, Figs. d, e; Pl. 37, Figs. a–f.

Type: Kennedy and Wright (1979) designated as lectotype the specimen illustrated by Stoliczka (1865: Pl. 60, Figs. 1, 1b).

Material and dimensions:

	D	H (%)	B (%)	U (%)
TA-R-417	rv1000	rv350 (35)	rv770 (77)	rv260 (26)
TA-R-619	rv760	rv285 (38)	rv730 (96)	rv195 (26)
TA-R-623	–	294	875	–
TA-S-563	989	359 (36)	933 (94)	343 (35)
TA-S-565	709	298 (42)	654 (92)	186 (26)

Description: involute ammonites with depressed and reniform whorl section, arched and continuous venter and flanks, and small and deep umbilici with flat, high and sloping walls and sharp umbilical shoulders. They reach their greatest whorl breadth close to the umbilical margins. Ornamentation is constituted by up to 40 low and fine ribs per whorl situated on the outer part of the flanks and the venter, and that weaken rapidly during ontogeny. They exhibit the early absence of umbilical tubercles, which is one of the main features of this unusual taxon.

Discussion: the difficult determination and classification of the species *F. rudra* (Stoliczka, 1865) has led to controversies among several authors. Kennedy and Wright (1979) considered that its weak and typical ribs are much more marked than those of other vascoceratids, but much more subdued than those of *F. superstes* (Kossmat, 1897). Furthermore, they indicated that the morphological features and the proportions of *F. rudra* and *F. bomba* (Eck, 1909) seem to coincide, suggesting the possibility that they might be synonyms. Meléndez-Hevia (1984) considered that the differentiation of the two latter species should not be exclusively based on the presence or absence of umbilical tubercles, because these structures are commonly developed by vascoceratids but they tend to disappear during growth. Kennedy et al. (1987) indicated that the lack of umbilical tubercles in *F. rudra*, as well as in *F. bomba*, *F. involuta* Barber, 1957, and *F. pervinquieri* Böse, 1920, could be a reason for assigning this species to the genus *Vascoceras* Choffat, 1898. Otherwise, Chancellor et al. (1994) pointed out that *F. bomba* could be a mere conspecific form of *F. superstes*.

On the question of whether *F. bomba* should be included in the synonymy of *F. rudra* or *F. superstes*, the sparse material obtained in Spain only indicates that the respective distributions of these taxa are very similar. In our view it is preferable to maintain the specific division between these taxa. On the other side, the presence of slender umbilical tubercles in the smallest specimen presented here, the ammonite TA-S-565 (Fig. 5(2–5)), seems to be especially significant in terms of the generic assignation of *F. rudra*. Likewise, the horizontal and vertical distributions of *F. rudra* in the Iberian Trough are coincident with those of the remaining species of *Fagesia* Pervinquière, 1907, and are geographically more extended and stratigraphically higher than those of the members of *Vascoceras*. Thus, despite the early loss of umbilical tubercles, *F. rudra* should not be assigned to the genus *Vascoceras*.

Lamolda et al. (1989) classified as *F.* aff. *F. tevesthensis* (Peron, 1896) several specimens obtained from the lower and middle Turonian of Ganuza, in the Outer Navarro-Cantabrian Platform, that were subsequently attributed to *F.* aff. *rudra* by Santamaría-Zabala (1991, 1995) because they show slightly stouter ribs, arising individually on the umbilical shoulders and extending all across the flanks and the venter, than the lectotype of the species of Stoliczka. In our opinion, these ammonites exhibit morphological features closer to *F. rudra* than to *F. tevesthensis*.

Occurrence: *F. rudra* has been identified in the upper part of the lower Turonian and the lower part of the middle Turonian of India, Spain, Madagascar, France and, possibly, Japan. In the Iberian Trough, it has been recognised in undetermined levels of the North-Ebro Area and in the lower part of the *Mammites nodosoides* zone of the Guadarrama Area.

Fagesia mortzestus sp. nov.

Figs. 7(1–4) and 8(1–4).

1984. *Fagesia* cf. *tehevensis* (Peron) – Meléndez-Hevia, p. 92, Pl. 11, Figs. 1a–c, 2 [only].

2006. *Fagesia* nov. sp. – Barroso-Barcenilla, p. 263, Pl. 38, Figs. a–d; Pl. 39, Figs. a–d; Pl. 40, Fig. a, Text-Fig. 72.

Types: specimen TA-S-564 (Fig. 8(1, 2)) is designated here as holotype. The paratypes are specimens CS-R-593, TA-R-582, TA-S-562 and TA-S-642.

Derivation of the name: it comes from the name of the ship in William Hope Hodgson's story titled "The ghost pirates" (1909).

Fig. 7. *Fagesia mortzestus* sp. nov., specimen TA-R-582, paratype, from the *Mammites nodosoides* subzone of Tamajón. 1. Apertural view. 2 and 3. Lateral views. 4. Ventral view. Bar scale = 5 cm.

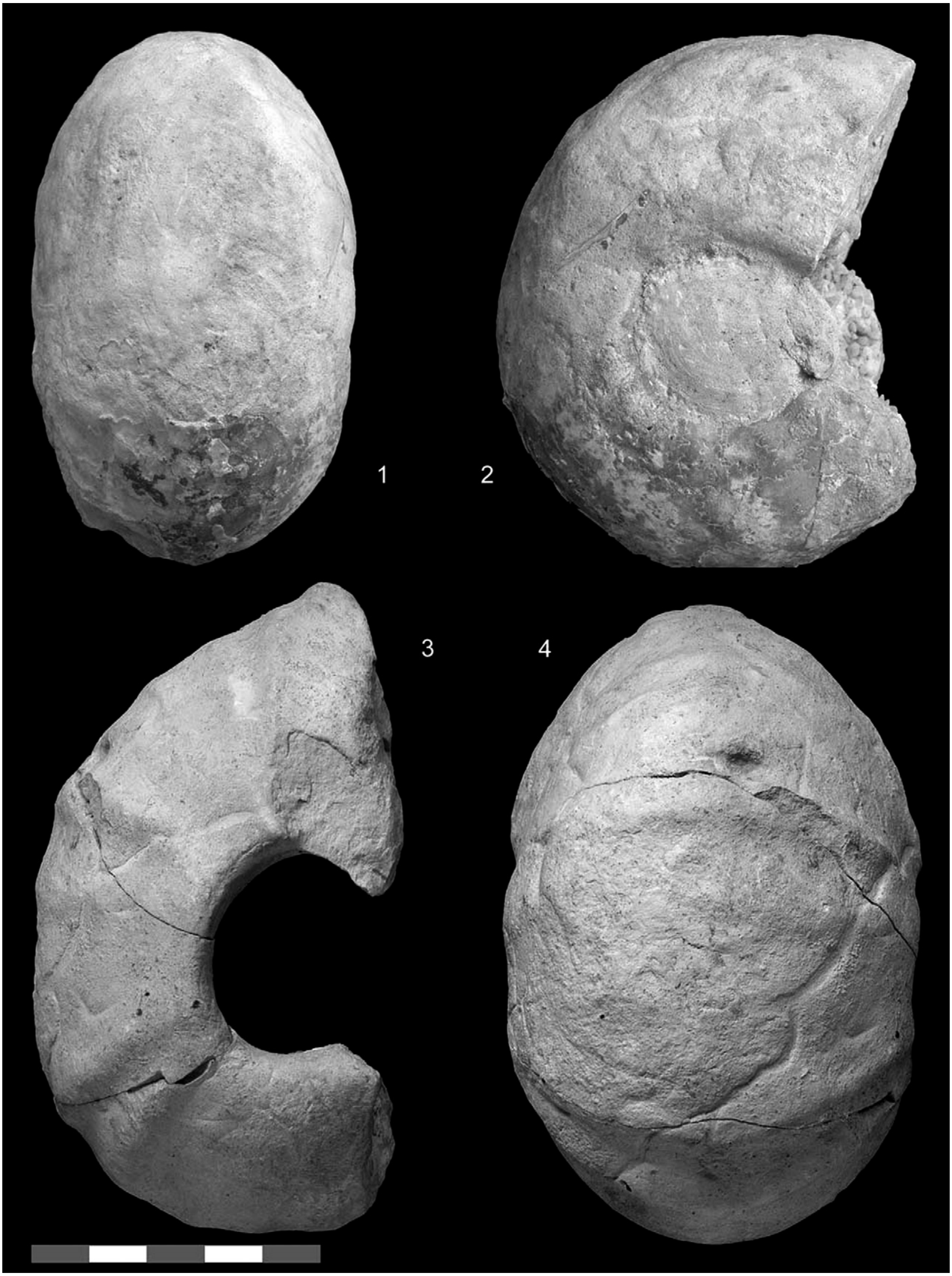

Fig. 8. *Fagesia mortzestus* sp. nov. 1, 2. Specimen TA-S-564, holotype, from the *Mammites nodosoides* subzone of Tamajón. 1. Ventral view. 2. Lateral view. 3, 4. Specimen CS-R-593, paratype, from an unknown lower Turonian level of Somolinos. 3. Lateral view. 4. Ventral view. Bar scale = 5 cm.

Material and dimensions:

	D	H (%)	B (%)	U (%)
CS-R-593	1215	510 (42)	786 (65)	352 (29)
TA-R-582	1094	442 (40)	615 (56)	342 (31)
TA-S-562	1174	488 (42)	766 (65)	350 (30)
TA-S-564	1038	470 (45)	606 (58)	330 (32)
TA-S-642	1099	467 (42)	712 (65)	304 (28)

Diagnosis: moderately depressed and slightly involute medium-sized ammonites with whorl from semicircular to subtriangular in section, bearing marked ribs and rounded umbilical tubercles as ornamentation. Tectiform ventral region, slightly convex fl and moderately broad umbilici for the genus *Fagesia* Pervinquière, 1907. The ornamentation becomes subdued during growth. The tubercles weaken or disappear on the last whorls, whereas the ribs, which decline, normally persist over the adult body chamber, and can remain as the only ornamentation at maturity. Suture lines relatively simple for the genus, each one with three high and broad saddles per fl nk.

Discussion: within the genus, *F. simplex* Barber, 1957, has subtriangular whorl section and tubercles, but develops more evolute coiling, lacks ribs and its simplified suture lines prompted Chancellor et al. (1994) to suggest the inclusion of this species in *Vascoceras* Choffat, 1898. *F. pervinquieri* Böse, 1920, shows morphology relatively close to that of *F. mortzestus*, but lacks umbilical tubercles, and *F. involuta* Barber, 1957, also presents slightly subtriangular whorls, although its shell is markedly globose, and it has a venter without ribs and a quite deep umbilicus. Among the remaining depressed members of *Fagesia* there are more ornamented taxa, as *F. catinus* (Mantell, 1822), *F. superstes* (Kossmat, 1897) and *F. siskiyouensis* Anderson, 1931; and less ornamented forms, like *F. rudra* (Stoliczka, 1865), *F. boucheroni* (Coquand, 1859), *F. peroni* Pervinquière, 1907, *F. fleuryi* Pervinquière, 1907, *F. bomba* (Eck, 1909) and *F. levis* Renz, 1982, but all of them possess rounded ventral regions. Thus, as their respective appearances are not tectiform, they can easily be distinguished from *F. mortzestus*. Otherwise, none of the relatively compressed forms of this genus, as *F. tevesthensis* (Peron, 1896), *F. haarmanni* Böse, 1920, *F. pachydiscoides* Spath, 1925, *F. californica* Anderson, 1931, *F. shastensis* Anderson, 1931, and the unusual and eccentric *F. lenticularis* Freund and Raab, 1969, have important morphological resemblances with *F. mortzestus*.

In the case of other genera, subtriangular forms like the one developed by *F. mortzestus* at maturity are also characteristic for *Choffaticeras* (*Choffaticeras*) *douvillei* (Peron, 1896) and *Vascoceras triangulare* Faraud, 1940, which were considered as synonyms by Kennedy (1994). These two taxa, however, are more involute, present more complex suture lines and lack umbilical tubercles and ribs, which this new species has. Likewise, the whorls of *V. obessum* (Taubenhaus, 1920), *V. ellipticum* Barber, 1957, and *V. costatum tectiforme* (Barber, 1957) have markedly triangular section, but these taxa are usually poorly ornamented with weaker and less persistent tubercles, and their umbilici are commonly narrower than the ones of *F. mortzestus*.

Occurrence: the specimens of this new species have been collected from the *M. nodosoides* subzone in localities of Somolinos, level 16 of Meléndez-Hevia (1984), and Tamajón, level 18 of Barroso-Barcenilla (2006), in the Guadarrama Area, located in the Iberian Trough, Spain.

Fagesia superstes (Kossmat, 1897)

Fig. 9(1, 2).

1897. *Olcostephanus superstes* – Kossmat, p. 26 (133), Pl. 4 (17), Fig. 1a–c.

1897. *Olcostephanus superstes* Kossmat – Peron, p. 84.

aff. 1898. *Ammonites* sp. indet. aff. *superstes* (Kossmat) – Choffat, p. 69, Pl. 10, Fig. 4.

1903a. *Pachyceras superstes* (Kossmat) – Pervinquière, pp. 96, 99, 101.

1907. *Fagesia superstes* (Kossmat) – Pervinquière, p. 322, Pl. 20, Figs. 1–4a, Text-Fig. 122 (included the *tunisiensis* and *spheroidalis* varieties).

1909. *Fagesia superstes* (Kossmat) – Eck, p. 182.

1912. *Fagesia superstes* (Kossmat) – Douvillé, p. 300, Text-Fig. 18.

1931. *Fagesia superstes* (Kossmat) – Basse, p. 39.

1940. *Fagesia superstes* (Kossmat) – Basse, p. 459.

1957. *Fagesia superstes* (Kossmat) – Moore in Wright, p. L420, Text-Fig. 541/2a–c.

1965. *Fagesia superstes spheroidalis* Pervinquière – Collignon, p. 46, Pl. 395, Fig. 1677.

cf. 1969. *Fagesia* cf. *F. superstes* (Kossmat) – Freund and Raab, p. 35, Text-Fig. 7f.

non 1969 *Fagesia superstes* (Kossmat) var. *tunisiensis* Pervinquière – Thomel, p. 116, Pl. d, Figs. 1, 2; Pl. e, Figs. 1, 2 (= *F. catinus*).

1978. *Fagesia spheroidalis* Pervinquière – Matsumoto and Muramoto, p. 282, Pl. 39, Fig. 1, Text-Fig. 2.

? aff. 1982. *Fagesia* aff. *superstes* (Kossmat) – Renz, p. 78, Pl. 22, Fig. 19a, b; Pl. 23, Fig. 4a, b, Text-Fig. 59b.

1983. *Fagesia superstes* (Kossmat) – Cobban and Hook, p. 16, Pl. 3, Figs. 1, 2; Pl. 13, Figs. 6–11, Text-Fig. 12.

1984. *Fagesia superstes* (Kossmat) – Meléndez-Hevia, p. 91, Pl. 10, Fig. 1a–c.

cf. 1989. *Fagesia* cf. *superstes* (Kossmat) – Luger and Gröschke, p. 372, Pl. 40, Figs. 1, 2.

aff. 1990. *Fagesia* aff. *superstes* (Kossmat) – Zaborski, Figs. 32, 33.

1990. *Fagesia superstes* (Kossmat) – Robaszynski et al., p. 266, Pl. 20, Fig. 1a, b; Pl. 21, Fig. 2a, b.

1994. *Fagesia superstes* (Kossmat) – Chancellor et al., p. 56, Pl. 13, Figs. 1, 2; Pl. 15, Figs. 4–9; Pl. 32, Fig. 4.

1996. *Fagesia superstes* (Kossmat) – Kaesler in Wright, p. 176, Text-Fig. 136/1a–c.

1997. *Fagesia superstes* (Kossmat) – Wiese, Pl. 2, Figs. 1, 2.

2001. *Fagesia superstes* (Kossmat) – Callapez and Ferreira, p. 84, Pl. 12, Fig. 3, Text-Figs. 23.7-8.

2006. *Fagesia superstes* (Kossmat) – Barroso-Barcenilla, p. 265, Pl. 40, Figs. b–d.

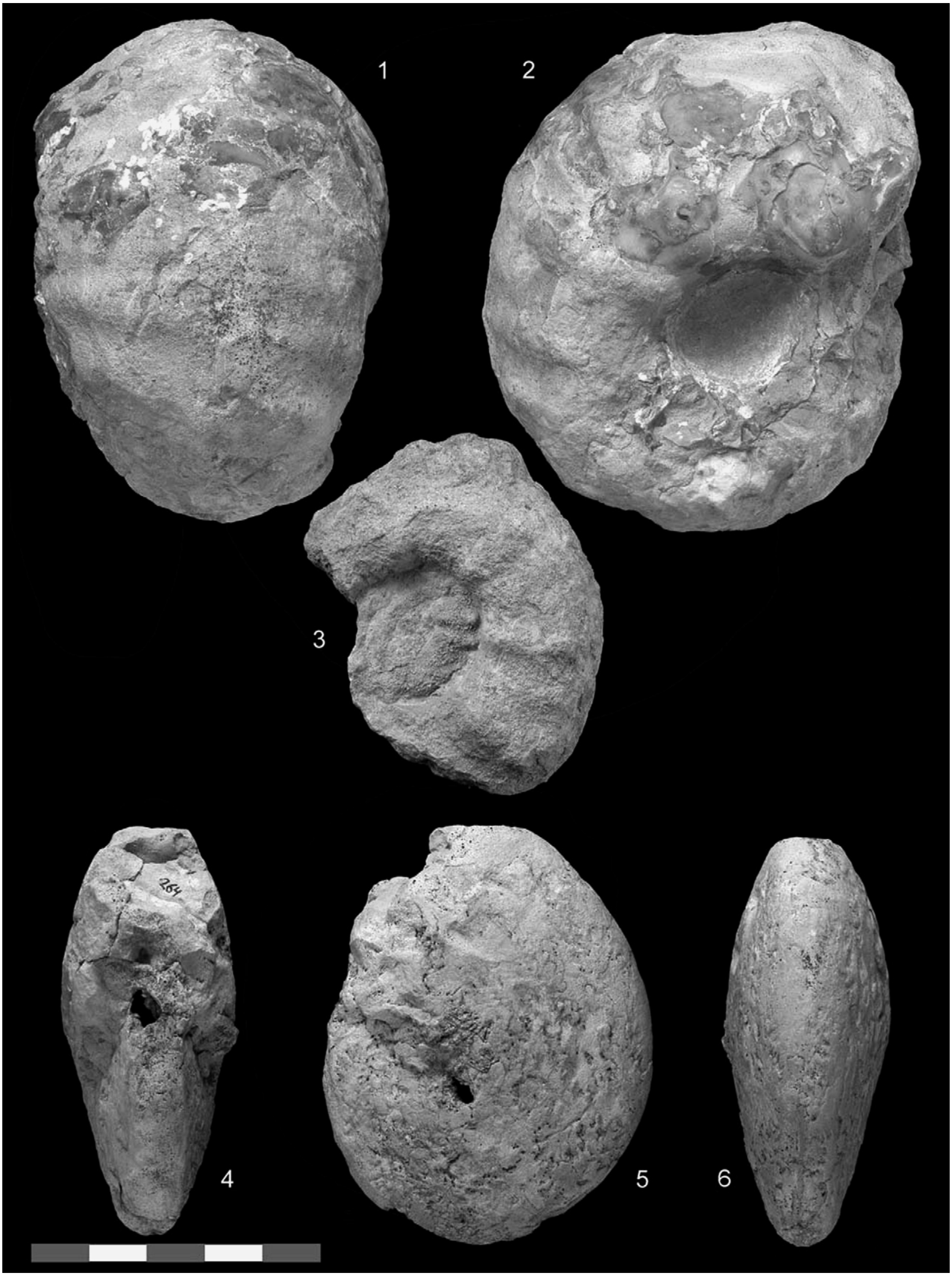

Fig. 9. 1, 2. *Fagesia superstes* (Kossmat, 1897), specimen TA-R-584, from the *Mammites nodosoides* subzone of Tamajón. 1. Ventral view. 2. Lateral view. 3. *Fagesia pachydiscoides* Spath, 1925, specimen CB-R-27, from an unknown lower Turonian level of Condemios, lateral view. 4, 5, 6. *Neoptychites cephalotus* (Courtiller, 1860), specimen PSR-264, from an unknown lower Turonian level of Soncillo. 4. Apertural view. 5. Lateral view. 6. Ventral view. The 5 cm bar scale only applies to Figs. 1–3; Figs. 4–6, x 3/4 with respect to the bar scale.

Type: the lectotype designated by Chancellor et al. (1994) is the original of Kossmat (1897: p. 26, Pl. 6(17), Fig. 1), probably from Odium, India.

Material and dimensions:

	D	H (%)	B (%)	U (%)
FT-S-697	836	rv318 (38)	–	rv340 (41)
FT-S-815	705	312 (44)	545 (77)	rv240 (34)
MS-7	609	281 (46)	514 (84)	215 (35)
PU-S-290	848	345 (41)	rv540 (64)	344 (41)
TA-R-419	580	220 (38)	rv365 (63)	198 (34)
TA-R-438	rv578	rv210 (36)	rv410 (71)	rv214 (37)
TA-R-584	953	414 (43)	630 (66)	228 (24)
TA-S-580	650	264 (41)	565 (87)	255 (39)

Description: cadiconic and slightly evolute or involute specimens with arched ventral region and moderately broad umbilici of high and vertical walls and rounded margins. They have a depressed and rounded subreniform whorl section, whose width is twice its height. Their marked ornamentation is made up by prominent and coarse ribbing and strong umbilical tubercles, each of them giving rise to two slightly prorsiradiate ribs that cross the flanks and continue without interruption over the ventral region. They possess relatively complex suture lines, with high saddles and asymmetric and bifid first lateral lobes. The rest of their lobes are commonly bifid.

Discussion: Kossmat (1897) described his new *Olcostephanus superstes*, but he did not establish subspecific divisions in this taxon. Pervinquière (1907) proposed his new varieties *F. superstes tunisiensis* and *F. superstes spheroidalis*, which present some slight differences from Kossmat's original. The first variety can be distinguished by having a rather more depressed whorl section and only 10–12 umbilical tubercles per whorl. *F. superstes spheroidalis* presents a rounded ventral region and a narrower umbilicus with only ten umbilical tubercles per whorl. In this respect it seems that the differences described above are not too significant, and that although certain authors, like Matsumoto and Muramoto (1978), gave specific status to the variety *spheroidalis*, it is preferable to consider these two morphological types of Pervinquière (1907) as simple intraspecific variants, as indicated by Cobban and Hook (1983) and Chancellor et al. (1994), among others.

Apart from strongly ornamented specimens that are more convergent with the holotype of *F. superstes*, other morphologies with weak ribs and relatively broad umbilici seem to be included within this species, like the ammonite of Peron (1897: p. 84) illustrated by Chancellor et al. (1994: Pl. 32, Fig. 4). These features are also very close to those of the specimens of *F.* aff. *superstes* of Renz (1982), although Kennedy et al. (1987) preferred to include them in the synonymy of *F. catinus* (Mantell, 1822).

F. superstes can easily be distinguished from *F. catinus* and *F. pachydiscoides* Spath, 1925, by its more globose morphology and its narrower umbilici. *F. rudra* (Stoliczka, 1865) almost lacks umbilical tubercles and has weak ribs that rapidly disappear during ontogeny, as opposed to *F. superstes*. *F. haarmanni* Böse, 1920, presents certain ornamentation that disappears during the early growing stages, whereas *F. involute* Barber, 1957, and *Fagesia peroni* Pervinquière, 1907, lack ribs.

With regard to the phylogeny of *F. superstes*, this species seems to be closely linked to *F. tevesthensis*, from which it may be derived by broadening of the whorl and a decline in ornamentation.

Occurrence: it has been found in biostratigraphic units equivalent to the lower Turonian *M. nodosoides* standard zone and in the lower part of the middle Turonian of India, Algeria, Portugal, Tunisia, Madagascar, Syria, Israel, Japan, the USA, Spain and, probably, Egypt and Venezuela. In the Iberian Trough, *F. superstes* occurs in the *M. nodosoides* zone of the Central Sector, whereas one member of this species has been collected from the same biostratigraphic unit of the North-Castilian Sector. It is the latest member of the genus *Fagesia* Pervinquière, 1907 identified in the present work.

Fagesia pachydiscoides Spath, 1925

Fig. 9(3).

1855. *Ammonites catinus* Mantell – Sharpe, p. 29, Pl. 13, Fig. 1a, b.

1925. *Fagesia pachydiscoides* – Spath, p. 198.

1978. *Fagesia pachydiscoides* Spath – Kennedy and Hancock, p. V19.

1981. *Fagesia pachydiscoides* Spath – Wright and Kennedy, p. 97, Text-Fig. 37.

1991. *Fagesia pachydiscoides* Spath – Santamaría-Zabala, p. 150, Pl. 9, Fig. 4.

cf. 1991. *Fagesia* cf. *pachydiscoides* Spath – Santamaría-Zabala, p. 152, Pl. 9, Fig. 5.

1992. *Fagesia catinus pachydiscoides* [sic] Spath – Thomel, p. 231, Pl. 87, Fig. 1; Pl. 88; Pl. 91, Figs. 1, 2; Pl. 92, 95; Pl. 96, Fig. 2.

1992. *Fagesia catinus niciensis* – Thomel, p. 232, Pl. 96, Fig. 1; Pl. 97–98; Pl. 99, Fig. 5.

1995. *Fagesia pachydiscoides* Spath – Santamaría-Zabala, p. 49, Pl. 2, Fig. 5.

2006. *Fagesia pachydiscoides* Spath – Barroso-Barcenilla, p. 268, Pl. 40, Fig. e.

Type: the holotype by monotypy is specimen 88583 of the BMNH, original of Sharpe (1855) and from the *M. nodosoides* zone of Wiltshire, UK.

Material and dimensions:

	D	H (%)	B (%)	U (%)
CB-R-27	675	rv232 (34)	rv230 (34)	rv241 (36)

Description: evolute specimen with rounded or subreniform whorl section hardly higher than wide, and relatively large umbilici with arched margins. The venter and flanks describe a continuous curved contour line, which makes it very difficult to establish one limiting trait separating them. The tubercles and, especially, the ribs weaken with growth, becoming an almost smooth or little ornamented body chamber.

Discussion: among other authors, Wright and Kennedy (1981), Chancellor (1982) and Kennedy et al. (1987) suggested that *F. pachydiscoides* Spath, 1925, may well be a synonym of

F. catinus (Mantell, 1822), and Thomel (1992) considered that the former taxon is a mere subspecies of the latter. The records of both taxa from the Iberian Trough are too poor to provide additional information to help in solving this matter. However, the morphologies of *F. catinus* and *F. pachydiscoides* seem easily distinguishable, which is why we have opted to maintain their specific division, agreeing with Santamaría-Zabala (1991, 1995). On the other hand, the ammonites assigned by Thomel (1992) to his new subspecies *F. catinus niciensis* seem to be evolute and compressed specimens of *F. pachydiscoides*.

The small or almost non-existent depression of the whorl, quite uncommon within the members of the genus *Fagesia* Pervinquière, 1907, and the evolute coiling allows for identification of this species. *F. catinus* shows a more depressed and involute whorl section, whereas *F. superstes* exhibits a coarser and more persistent ornamentation, and a higher number of umbilical tubercles per whorl.

Occurrence: Lower Turonian of the UK, Spain and France. In the Iberian Trough, the specimen identified by Santamaría-Zabala (1991, 1995) and the one presented herein come from undetermined lower Turonian levels. In the first case of the Outer Navarro-Cantabrian Platform, and in the second case of the Guadarrama Area.

Neoptychites Kossmat, 1895

[*Betiokytes* Collignon, 1965, p. 56, type species by original designation *Hemitissotia* (*Betiokytes*) *besairiei* Collignon, 1965. *Pseudoneoptychites* Leanza, 1967, p. 202, type species by original designation *Pseudoneoptychites andinus* Leanza, 1967].

Type species: *Ammonites telinga* Stoliczka, 1865, synonym of *Ammonites cephalotus* Courtiller, 1860. Several authors indicated that the designation is original. However, Kossmat (1895) did not clearly select the species of Stoliczka as the type of his new group. Solger (1904: p. 105) was the first author to consider *A. telinga* as generotype of *Neoptychites*, as indicated by Chancellor et al. (1994) and Kaesler in Wright (1996).

Diagnosis: evolute and medium-sized group with variably compressed whorls, reaching their greatest breadth near the arched umbilical margins, and small crateriform umbilici occasionally covered by an umbilical lid. Its venter is narrow and rounded or slightly tabulate, and its flanks are flat. Some of its species may have ribs, which are annular, broad and low, and constrictions or small and elongated umbilical tubercles on the inner whorls. These ornamental elements disappear quite soon, leaving the outer whorls totally smooth. The adult body chamber usually has contracted apertures. Although the suture lines of this genus are highly variable, they are among the most complex ones of the family Vascoceratidae Douvillé, 1912, presenting large, broad and low sutural elements.

Discussion: the morphology of its shell, with the typical aperture, and the absence of tubercles from early ontogenetic stages clearly distinguishes this genus from *Vascoceras* Choffat, 1898. The suture lines are markedly simpler than those of *Choffaticeras* Hyatt, 1903. Otherwise, *Neoptychites* bears some resemblances to *Thomasites*, as Pervinquière (1907) emphasised when he described his new genus. Considering this, Freund and Raab (1969) noted that, although the adult morphology of *Neoptychites* may be similar to that of *Thomasites*, they have markedly different ornamentations and suture lines. Chancellor et al. (1994) wrote a detailed description of the features distinguishing both genera.

Although, as indicated above, the identification of *Neoptychites* is relatively easy, the differentiation between the species assigned to this genus can be quite hard, as their distinction is only based on the dimensions of the whorl breadth and certain details of the suture lines and of the juvenile ornamentation that can hardly be observed in some mature specimens.

In relation to the synonymy of the genus, Kennedy and Wright (1979) considered that the description of *Pseudoneoptychites* is based on a juvenile specimen of *Neoptychites*. Therefore, they indicated that the group of Leanza should be considered as a mere synonym of the genus of Kossmat. These authors also preferred to regard *Betiokytes* as a subgenus of *Neoptychites* that groups species with subtabular venter and suture lines with wide, rounded or slightly incised saddles. Nevertheless, most subsequent authors opted for not differentiating subgenera within *Neoptychites*. Kaesler in Wright (1996) also included *Franciscoites* in the synonymy of *Neoptychites*, although he did not justify the reasons for this decision. In our opinion, the original descriptions of *Betiokytes* and of *Pseudoneoptychites* are, respectively, based on an adult specimen and on several juvenile members of *Neoptychites*. Likewise, the scarce relevance of the diagnostic features of *Franciscoites* remarked on by its author does not seem to justify the generic separation of this group. Therefore, *Betiokytes*, *Pseudoneoptychites* and, possibly, *Franciscoites* should simply be regarded as synonyms of *Neoptychites*.

Concerning the phylogeny of the genus, many authors remarked on the isolated position of *Neoptychites* within the Vascoceratidae, because transitional forms with other genera were never identified. Some palaeontologists, like Pervinquière (1907), Diener (1925) and Basse (1931), excluded *Neoptychites* from the Vascoceratidae. Nevertheless, nowadays it is a commonly accepted opinion that the morphologic proximity and the phylogenetic relationship of *Neoptychites* to other members of the Vascoceratidae are both valid arguments for attributing the genus of Kossmat to the family of Douvillé.

Occurrence: it has been identified from lower to upper Turonian of France, Spain, Portugal, Morocco, Algeria, Tunisia, Egypt, Cameroon, Nigeria, Madagascar, Syria, Israel, India, Japan, the USA, Mexico, Trinidad and Tobago, Brazil, Colombia and Venezuela, reaching its maximum abundance in the lower part of the middle Turonian. The specimens of *Neoptychites* from the Iberian Trough have been obtained almost exclusively within the *Mammites nodosoides* zone and the middle Turonian from the Outer Navarro-Cantabrian Platform and the North-Castilian Sector.

Neoptychites cephalotus (Courtiller, 1860)

Fig. 9(4–6) and Fig. 10(1–3).

1850. *Ammonites santonensis* – d'Orbigny, p. 212.

1860. *Ammonites cephalotus* – Courtiller, p. 248, Pl. 2, Figs. 1, 4.

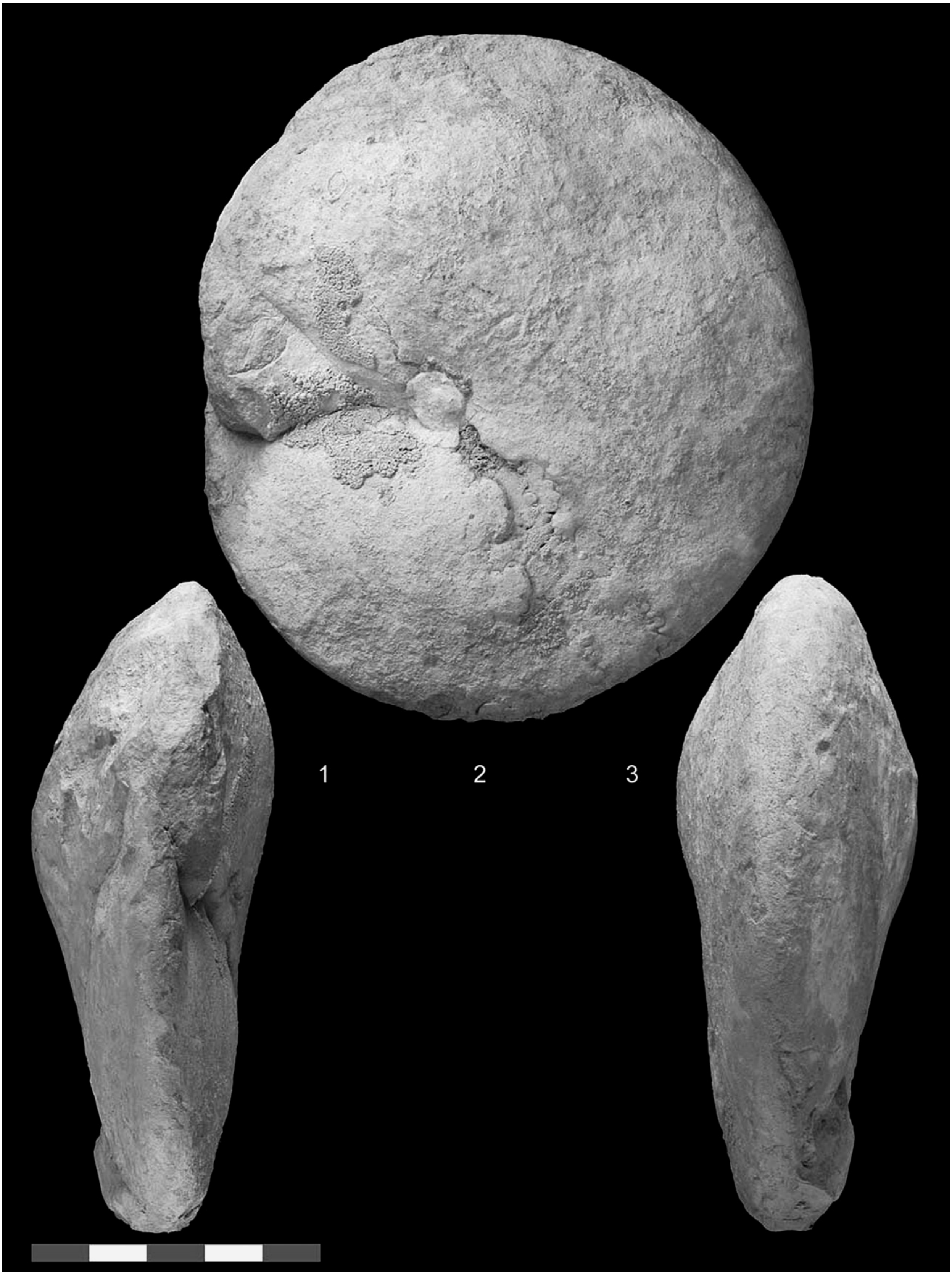

Fig. 10. *Neoptychites cephalotus* (Courtiller, 1860), specimen PU-S-382, from the *Mammites nodosoides* zone of Puentedey, x 3/4 with respect to the 5 cm bar scale. 1. Apertural view. 2. Lateral views. 3. Ventral view.

1865. *Ammonites xetra* – Stoliczka, p. 124, Pl. 61, Figs. 1, 2.

1865. *Ammonites telinga* – Stoliczka, p. 125, Pl. 62, Figs. 1, 2.

1867. *Ammonites cephalotus* Courtiller – Courtiller, p. 3, Pl. 1, Figs. 1–3; Pl. 2, Figs. 1, 2.

1889. *Pachydiscus africanus* – Peron, p. 28, Pl. 17, Figs. 9, 10.

1895. *Neoptychites telinga* (Stoliczka) – Kossmat, p. 71, Pl. 7, Fig. 1.

1895. *Neoptychites xetra* (Stoliczka) – Kossmat, p. 72.

1896. *Neoptychites cephalotus* (Courtiller) – de Grossouvre, p. 86.

1896. *Neoptychites telinga* (Stoliczka) – Peron, p. 38, Pl. 6, Fig. 1; Pl. 7, Fig. 1; Pl. 17, Fig. 13.

1897. *Pulchellia perovalis* – von Koenen, p. 10, Pl. 1, Fig. 3; Pl. 2, Fig. 6.

? 1903a. *Neoptychites* cf. *N. xetra* (Stoliczka) – Pervinquière, p. 101.

1903b. *Neoptychites cephalotus* (Courtiller) – Pervinquière, fiche 5, 5c.

1904. *Neoptychites telingaeformis* – Solger, p. 108, Pl. 3, Figs. 2, 3, Text-Figs. 9–17 (included the *elegans*, *palmata* and *discrepans* varieties).

1904. *Neoptychites crassus* – Solger, p. 119, Pl. 3, Fig. 5a, b, Text-Figs. 18, 19 (included the *crassus* and *asymetrica* varieties).

1904. *Neoptychites perovalis* (von Koenen) – Solger, p. 122.

1907. *Neoptychites cephalotus* (Courtiller) – Pervinquière, p. 393, Pl. 27, Figs. 1–4, Text-Fig. 152.

? 1907. *Neoptychites xetriformis* – Pervinquière, p. 398, Pl. 27, Figs. 5–7, Text-Figs. 153, 154.

1907. *Neoptychites gourguechoni* – Pervinquière, p. 400, Pl. 27, Figs. 8, 9, Text-Figs. 155, 156.

1912. *Neoptychites cephalotus* (Courtiller) – Roman, p. 13, Pl. 1, Fig. 2.

? aff. 1920. *Neoptychites* aff. *xetriformis* Pervinquière – Böse, p. 223, Pl. 18, Figs. 9, 11, Text-Fig. 7.

? 1920. *Neoptychites xetriformis* Pervinquière – Taubenhaus, p. 45, Pl. 5, Fig. 1.

1931. *Neoptychites cephalotus* (Courtiller) – Basse, p. 34, Pl. 4, Fig. 9; Pl. 11, Fig. 5a, b.

? 1931. *Neoptychites xetriformis* Pervinquière – Basse, p. 35, Pl. 12, Fig. 1.

1931. *Neoptychites cephalotus* (Courtiller) – Basse, p. 47, Text-Fig. 2a, b.

? 1931. *Neoptychites* sp. aff. *gourguechoni* Pervinquière – Adkins, p. 57, Pl. 2, Figs. 18, 20.

1932. *Neoptychites telingaeformis* Solger var. *discrepans* Solger – Riedel, p. 123, Pl. 26, Fig. 5.

1932. *Neoptychites perovalis* (von Koenen) – Riedel, p. 123, Pl. 26, Fig. 7.

1935. *Neoptychites cephalotus* (Courtiller) – Karrenberg, p. 143, Fig. 4.

1939. *Neoptychites cephalotus* (Courtiller) – Basse, p. 47, Text-Fig. 2.

1940. *Neoptychites cephalotus* (Courtiller) – Basse, p. 456, Pl. 5, Fig. 4a, b.

? cf. 1954. *Neoptychites* cf. *N. xetriformis* Pervinquière – Kummel and Decker, p. 315, Pl. 32, Fig. 3, Text-Figs. 5, 6.

1955. *Neoptychites perovalis* (von Koenen) – Reyment, p. 66, Pl. 10, Fig. 4, Text-Fig. 29.

1955. *Neoptychites telingaeformis* Solger – Reyment, p. 66, Pl. 15, Fig. 1, Text-Fig. 30 [*non* Pl. 11, Fig. 4].

1955. *Neoptychites crassus* Solger – Reyment, p. 67.

1957. *Neoptychites cephalotus* (Courtiller) – Moore in Wright, p. L422, Text-Fig. 540/6a, b.

1960a. *Neoptychites cephalotus* (Courtiller) – Wiedmann, pp. 711–712, 715, 719, 721.

? 1963b. *Neoptychites xetriformis* Pervinquière – Powell, p. 1229, Pl. 171, Figs. 2–4, Text-Fig. 5b.

1964. *Neoptychites cephalotus* (Courtiller) – Wiedmann, pp. 111–112, 114, 115.

1965. *Neoptychites cephalotus* (Courtiller) – Collignon, p. 58, Pl. 401, Fig. 1685.

1966. *Neoptychites cephalotus* (Courtiller) – Collignon, p. 43, Pl. 24, Fig. 1a, b.

1969. *Neoptychites cephalotus* (Courtiller) – Freund and Raab, p. 48.

? 1969. *Neoptychites xetriformis* Pervinquière – Freund and Raab, p. 48.

cf. 1969. *Neoptychites* cf. *N. xetra* (Stoliczka) – Freund and Raab, p. 49, Text-Fig. 10d.

? 1969. *Neoptychites* sp. 1 – Freund and Raab, p. 49, Text-Fig. 10e, f.

? 1969. *Neoptychites* sp. 2 – Freund and Raab, p. 59, Text-Fig. 10 g.

? 1972. *Neoptychites xetriformis* Pervinquière – Cobban and Scott, p. 89, Pl. 30, Figs. 2–6, Text-Fig. 48.

cf. 1972. *Neoptychites* cf. *N. cephalotus* (Courtiller) – Cobban and Scott, p. 90, Pl. 30, Fig. 9, Text-Figs. 49, 50.

1975a. *Neoptychites cephalotus* (Courtiller) – Wiedmann, p. 141.

1978. *Neoptychites cephalotus* (Courtiller) – Matsumoto, p. 197, Pl. 1, Fig. 1, Text-Fig. 1.

1978. *Neoptychites* (*Neoptychites*) *cephalotus* (Courtiller) – Wiedmann and Kauffman, Pl. 10, Fig. 2.

1979. *Neoptychites* (*Neoptychites*) *cephalotus* (Courtiller) – Wiedmann, Pl. 10, Fig. 2.

1979. *Neoptychites cephalotus* (Courtiller) – Kennedy and Wright, p. 670, Pl. 82, Figs. 3–5; Pl. 83, Figs. 1–3; Pl. 84, Fig. 3; Pl. 85, Figs. 1–5; Pl. 86, Figs. 4, 5, Text-Fig. 2.

? 1979. *Neoptychites xetriformis* Pervinquière – Kennedy and Wright, p. 679, Pl. 84, Figs. 1, 2; Pl. 86, Figs. 1–3.

1982. *Neoptychites cephalotus* (Courtiller) – Matsumoto and Obata, p. 78, Pl. 4, Fig. 1a, d.

1982. *Neoptychites cephalotus* (Courtiller) – Amédro and Badillet in Robaszynski et al., p. 131, Pl. 2, Fig. 1a, b.

? 1982. *Neoptychites xetriformis* Pervinquière – Amédro and Badillet in Robaszynski et al., p. 131, Pl. 2, Figs. 2a, b.

aff. 1982. *Neoptychites* aff. *crassus* Solger – Renz, p. 88, Pl. 26, Fig. 16a, b.

aff. 1982. *Neoptychites* aff. *telingaeformis discrepans* Solger – Renz, p. 88, Pl. 26, Fig. 17.

? 1982. *Neoptychites transitorius* – Renz, p. 87, Pl. 26, Figs. 15a, b, 18a, b, Text-Figs. 66a, 65d.

? 1982. *Neoptychites xetriformis* Pervinquière – Renz, p. 88, Pl. 26, Fig. 19a, b, Text-Fig. 67.

? 1983. *Neoptychites cephalotus* (Courtiller) – Cobban and Hook, p. 14, Pl. 3, Figs. 9–11; Pl. 9–12, Text-Fig. 11.

1985. *Neoptychites cephalotus* (Courtiller) – Amédro and Hancock, Fig. 7c, d.

1987. *Neoptychites cephalotus* (Courtiller) – Zaborski, p. 43, Figs. 31, 32.

? 1988. *Neoptychites cephalotus* (Courtiller) – Kennedy and Cobban, p. 604, Pl. 3, Figs. 3, 4, 8, 9.

cf. 1989. *Neoptychites* cf. *cephalotus* (Courtiller) – Kennedy et al., p. 84.

? 1989. *Neoptychites cephalotus* (Courtiller) – Cobban et al., p. 54, Figs. 54, 88bb–ff.

1990. *Neoptychites cephalotus* (Courtiller) – Zaborski, Fig. 31.

1990. *Neoptychites cephalotus* (Courtiller) – Robaszynski et al., p. 266, Pl. 20, Figs.?2a, b, 3a, b; Pl. 21, Fig.? 3a, b.

? 1992. *Neoptychites xetriformis* Pervinquière – Thomel, p. 234, Pl. 103, Figs. 1–3.

1994. *Neoptychites cephalotus* (Courtiller) – Chancellor et al., p. 70, Pl. 16, Figs.?1–3, 4–6,?7–9; Pl. 17, Figs. 1–5; Pl. 18, Figs. 1–3; Pl. 26, Figs. 2–4.

1994. *Neoptychites* gr. *cephalotus* (Courtiller) – Meister et al., p. 206, Pl. 14, Fig. 4, Text-Fig. 10.

? 1994. *Neoptychites xetriformis* Pervinquière – Kassab, p. 121, Fig. 5(5–7).

1996. *Neoptychites* gr. *cephalotus* (Courtiller) – Meister and Abdallah, p. 11, Pl. 3, Fig.?2; Pl. 5, Fig. 3; Pl. 6, Fig. 1, Text-Figs. 5f, g.

1996. *Neoptychites cephalotus* (Courtiller) – Kaesler in Wright, p. 176, Text-Fig. 136/2a, b.

1998. *Neoptychites cephalotus* (Courtiller) – Callapez, Pl. 13, Figs. 7, 8; Pl. 14, Fig. 6.

2001. *Neoptychites cephalotus* (Courtiller) – Callapez and Ferreira, p. 89, Pl. 13, Figs. 7, 8; Pl. 14, Fig. 6, Text-Figs. 23.11, 12.

2005. *Neoptychites* gr. *cephalotus* (Courtiller) – Meister and Abdallah, p. 136, Pl. 15, Figs. 1,?2; Pl. 16, Fig. 1; Pl. 20, Fig. 1.

2006. *Neoptychites cephalotus* (Courtiller) – Barroso-Barcenilla, p. 273, Pl. 41, Figs. a–e; Pl. 42, Figs. a–c, Text-Fig. 74.

Type: the lectotype designated by Kennedy and Wright (1979: p. 671, Pl. 83, Figs. 1–3) is the specimen 631 of the CS, original of Courtiller (1860: Pl. 2, Figs. 1, 2), collected from the middle Turonian of the surroundings of Saumur, France.

Material and dimensions:

	D	H (%)	B (%)	U (%)
FT-R-742	1325	713 (54)	576 (43)	105 (8)
PS-R-264	1006	596 (59)	426 (42)	69 (7)
PU-R-248	1235	627 (51)	417 (34)	61 (5)
PU-S-382	1640	855 (52)	622 (38)	139 (8)
PU-S-384	1054	521 (49)	rv290 (28)	72 (7)

Description: involute and compressed specimens with suboval or subtriangular whorl section and smooth surface at maturity. They have rounded and narrow ventral region, convergent and flat or slightly convex flanks and very small umbilici. Some mature specimens develop a broad bulge on each flank of the body chamber, which provides them with a typical fusiform profile. They present relatively variable suture lines.

Discussion: de Grossouvre (1896), like almost all the authors who have studied this species, considered that *A. telinga* Stoliczka, 1865, can be included in the normal morphological variability of *Neoptychites cephalotus* (Courtiller, 1860). Pervinquière (1907) noted that *Pachydiscus africanus* Peron, 1889, *A. xetra* Stoliczka, 1865, and *N. telingaeformis* Solger, 1904, have many resemblances to *N. cephalotus*, and included the first taxon and, with doubts, the third one in the synonymy of this species. Kennedy and Wright (1979) agreed with Pervinquière (1907), and indicated that the original descriptions of *A. xetra* and *P. africanus* would be based respectively on a broad mature specimen and on a juvenile member of *N. cephalotus*. They also considered that *N. telingaeformis* and *N. crassus* Solger, 1904, including its respective varieties, as well as *Pulchellia perovalis* von Koenen, 1897, and *N. gourguechoni* Pervinquière, 1907, are synonyms. These taxonomic suggestions were subsequently maintained by Kennedy and Cobban (1988) and Kennedy et al. (1989), among others. Likewise, Kennedy and Wright (1979) illustrated the holotype of *A. santonensis* d'Orbigny, 1850. They also transcribed the original description of this taxon that, on the basis of the opinion 126 of the ICZN, they considered invalid. Finally, these authors assigned the ammonite attributed to *N. telingaeformis* by Reyment (1955) to the species *Hoplitoides gibbulosus* (von Koenen, 1897), and considered the specimens classified as *N.* cf. *N. xetra*, *N.* sp. 1 and *N.* sp. 2 by Freund and Raab (1969) as probable members of *N. cephalotus*. Zaborski (1987) and Chancellor et al. (1994) added two other taxa to the already large list of synonyms of *N. cephalotus* accepted by Kennedy and Wright (1979). *Franciscoites suarezi* Etayo-Serna, 1979, known only by a small number of juvenile specimens, was considered as a possible synonym of *N. cephalotus* by both authors. *N. transitorius* Renz, 1982, was suggested as a probably conspecific form of *N. cephalotus* by Zaborski (1987), and was unequivocally included in the synonymy of the same species by Chancellor et al. (1994).

In fact, the original of *A. telinga* shows the typical features of the lectotype of *N. cephalotus*, including the characteristic lateral inflation of the adult body chamber. No distinction can therefore be made between these two taxa. In a similar way, observing the available images of the type of *A. santonensis*, this taxon does not seem distinguishable from *N. cephalotus*. In addition, the morphology and the ontogenetic development shown by the lectotype of *A. xetra* designated by Kennedy and Wright (1979) appear to indicate that it is a wide specimen of *N. cephalotus*. After studying the small type of *P. africanus* and the two types of *N. gourguechoni* in the MNHN, we have noticed that these ammonites possess, respectively, the typical features of the juvenile and of the compressed members of

N. cephalotus. Likewise, the morphologies of the three new taxa proposed by Solger (1904) also seem to coincide with *N. cephalotus*. Specifically, the features of *N. crassus* are coincident with those of the more depressed specimens of *N. cephalotus* before losing ornamentation. The proportions and suture lines of *N. telingaeformis* and *N. perovalis* apparently also correspond to members of *N. cephalotus*. In addition to these morphological observations it should be mentioned that the only record of *N. telingaeformis* from the Iberian Trough is within the geographical and stratigraphical distribution attributed to *N. cephalotus*.

The types of *N. transitorius* are small specimens, still with constrictions, whose features coincide with those of the representatives of *N. cephalotus* in the early ontogenetic stages. Finally, it should be emphasised that the specimen assigned to *N. telingaeformis* by Reyment (1955) shows suture lines notably different from those of the members of Vascoceratidae, whereas the ammonites classified as *N.* cf. *N. xetra*, *N.* sp. 1 and *N.* sp. 2 by Freund and Raab (1969) seem to be representatives of *N. cephalotus*.

The relationship between *N. cephalotus* and *N. xetriformis* has caused much controversy. Kennedy and Wright (1979), and subsequently Robaszynski et al. (1982), Zaborski (1987) and Thomel (1992), among others, maintained that both taxa should be regarded as different species on the basis of the more distant ribbing, which extends up to the adult body chamber, and the smaller size of *N. xetriformis*. However, these authors suggested that *N. cephalotus* and *N. xetriformis* could be two mere dimorphs. On the contrary, other authors, like Cobban and Hook (1983), Kennedy and Cobban (1988), Cobban et al. (1989), Robaszynski et al. (1990) and Chancellor et al. (1994), considered that these two taxa may represent the macroconchs (*N. cephalotus*) and the microconchs (*N. xetriformis*) of the species of Courtiller. It has recently been observed by the authors of the present work that the persistent and striking ornamentation and the broad whorl section of the three original specimens of *N. xetriformis*, currently held in the MNHN, make it easy to differentiate them from the lectotype of *N. cephalotus*. Nevertheless, many works have shown the wide morphological variability of *N. cephalotus*, in which *N. xetriformis* could probably be included as a mere dimorph. Therefore, the specimens classified as *N. xetriformis*, or morphologically very close to this taxon, although with doubts, have been included here in the synonymy of *N. cephalotus*.

Occurrence: this species has been identified in the lower and middle Turonian of France, southern India, Tunisia, Algeria, Cameroon, Madagascar, Spain, Syria, Israel, Morocco, the USA, Japan, Nigeria, Egypt, Portugal and, possibly, Mexico and Venezuela. The oldest records of *N. cephalotus* have been collected from the *Pseudaspidoceras flexuosum* zone of the USA, as noticed by Cobban and Scott (1972) and Kauffman et al. (1978). In other countries this species occurs in biostratigraphic units equivalent to the upper part of the *Watinoceras devonense* standard zone and to the *M. nodosoides* and *Collignoniceras woollgari* standard zones. In the Iberian Trough, although Wiedmann and Kauffman (1978) and Wiedmann (1979) assigned this species to their middle Turonian zone T VI, we have demonstrated that the stratigraphical distribution of *N. cephalotus* in this region also comprises the lower Turonian *M. nodosoides* zone. Except for one, all the specimens of *N. cephalotus* come from the Outer Navarro-Cantabrian Platform and the North-Castilian Sector.

5. Conclusions

In the present work, new specimens from the Iberian Trough have been described and assigned to the species *F. catinus*, *F. tevesthensis*, *F. rudra*, *F. mortzestus* sp. nov., *F. superstes*, *F. pachydiscoides* and *N. cephalotus*. Although all these taxa had already been cited, except for the logical exception of the new species, *F. catinus* and *F. tevesthensis* had never previously been properly classified nor illustrated for this palaeogeographical region. During the revision, it has been noted the presence of specimens that are attributable to *F. bomba* in the collections of the UT and the UCM. Therefore, it can be assumed that the family Vascoceratidae is represented, among others, by the genera *Fagesia* and *Neoptychites* in the Iberian Trough, where the species *F. catinus*, *F. tevesthensis*, *F. rudra*, *F. mortzestus* sp. nov., sp. nov., *F. superstes*, *F. pachydiscoides*, *N. cephalotus* and, probably, *F. bomba* have been properly identified.

Furthermore, the distribution of the members of the Vascoceratidae presented here has been determined (Fig. 11). Although one member of the genus *Fagesia*, attributed to *F. catinus*, has been collected in the *Spathites* (*Jeanrogericeras*) *subconciliatus* zone, the continuous occurrence of this group in this palaeogeographical region has been observed in the upper part of the *Choffaticeras* (*Leoniceras*) *luciae* subzone and the *M. nodosoides* zone. To be more precise, *F. tevesthensis* has been identified in the upper part of the *Choffaticeras* (*Leoniceras*) *luciae* subzone and the base of the *M. nodosoides* subzone. *F. mortzestus* sp. nov. and *F. rudra* have been obtained in the *M. nodosoides* subzone. Lastly, the species *F. superstes* has been identified in the upper part of the *M. nodosoides* subzone and in the *Wrightoceras munieri* subzone, and consequently its stratigraphically highest records seem to determine the end of the occurrence of *Fagesia* in the Iberian Trough.

Otherwise, the only species of *Neoptychites* identified in this palaeogeographical region, *N. cephalotus*, has been recorded in the *M. nodosoides* zone and levels attributed to the middle Turonian. The highest specimens of this genus can be considered as the latest members of the Vascoceratidae in the Iberian Trough.

In terms of the phylogeny of the group, one possible evolutionary lineage joining *F. tevesthensis* and *F. superstes* has been identified within the genus *Fagesia* (Fig. 11). It progressively becoming more involute and depressed, and less ornamented forms.

After observing the distribution of the Vascoceratidae in the Iberian Trough, three main evolutionary phases can be distinguished, as already pointed out by Barroso-Barcenilla and Goy (2005). The last one occurs subsequently to the successive dominances of the ‘‘primitive’’ *Vascoceras* and of

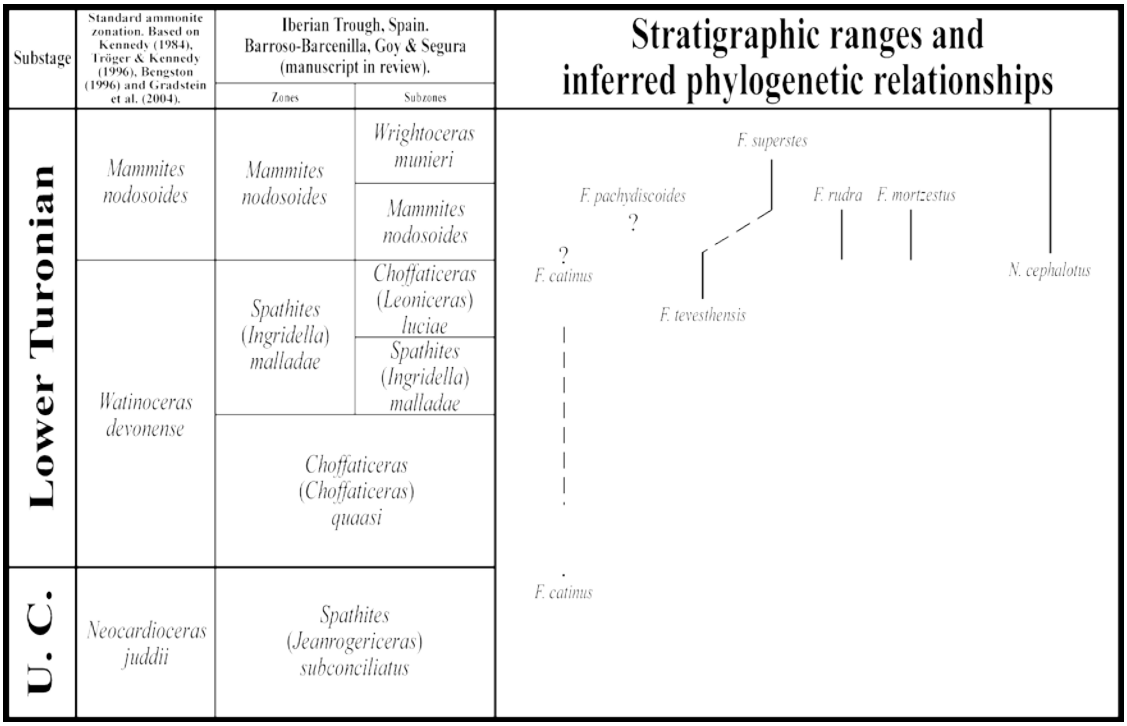

Fig. 11. Stratigraphical ranges of the species of *Fagesia* and *Neoptychites* identified in this work and their inferred phylogenetic relationships.

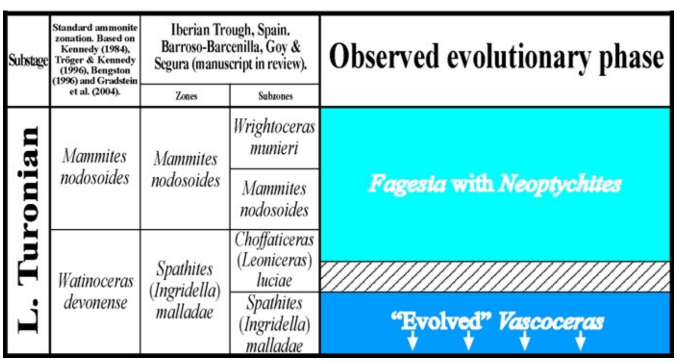

Fig. 12. Observed phase in the evolution of Vascoceratidae (*Fagesia* and *Neoptychites*) in the Iberian Trough.

the "evolved" *Vascoceras*, analysed in detail by Barroso-Barcenilla and Goy (manuscript in review), and is characterised by the dominance of *Fagesia* and *Neoptychites* (Fig. 12). This phase has been identified in the upper part of the *Choffaticeras* (*Leoniceras*) *luciae* subzone, and mainly in the *M. nodosoides* zone of the lower Turonian. During this phase, species of the genera *Fagesia* and *Neoptychites* as *F. tevesthensis*, *F. rudra*, *F. mortzestus* sp. nov., *F. superstes* and *N. cephalotus*, represent the Vascoceratidae. This evolutionary phase seem not only to coincide with the evolutionary interval followed by the family in other palaeogeographical regions, but also by other groups, as indicated by Barroso-Barcenilla and Goy (2005).

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